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Production of a Population of the Stout Razor Clam (Tagelus plebeius Solander) in a Virginia Estuary

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PRODUCTION OF A POPULATION OF THE STOUT RAZOR CLAM (*TAGELUS PLEBEIUS* SOLANDER) IN A VIRGINIA ESTUARY

by

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Dr. Anthony J. Provenzano, Jr.
Director

ABSTRACT

PRODUCTION OF A POPULATION OF THE
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IN A VIRGINIA ESTUARY

Mark James Grussendorf
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The annual net secondary production of the stout razor clam, Tagelus plebeius, was estimated at three sites on an intertidal sand flat at Lynnhaven Inlet, Virginia. Samples were taken at six week intervals for one year. The range of net production (P), mean annual biomass (B), and P/B ratios was 18.3-28.7 g $m^{-2}year^{-1}$, 27.2-53.3 g m^{-2}, and 0.54-0.67, respectively. The total biomass did not show significant seasonal variation though differences between sites were significant. Production varied temporally but was not significantly different between sites. The P/B ratios were high in the younger year-classes but low in the older year-classes. Recruitment was bimodal in 1977 but unimodal in 1978. Growth was fast in the first year of life with more than half of the total shell growth achieved prior to the first winter. Growth and maximum shell length did not vary significantly between sites. Though mean grain size and sorting coefficients were significantly different between sites, the absolute differences in magnitude were small and not considered to be biologically significant for Tagelus plebeius. Production, biomass, and P/B ratios were computed at various sample intervals with only small differences noted using 12 and 24 week intervals. With the 52 week interval, differences were extreme. Deep burrows and very low concentrations

of organic material in the sediment may be important factors contributing to the high abundance of Tagelus plebeius on the sand flat. Deep burrows facilitate predator evasion and buffer changes in the physical environment, while the low organic content of the sediment is not conducive to deposit feeders that might upset the burrows of Tagelus plebeius

To my son Christopher, who likes to dig for clams and catch crabs .

ACKNOWLEDGMENTS

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My wife, Vicki, has been instrumental in encouraging me to complete this project. Her help in arranging and proofreading the manuscript has been invaluable.

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INTRODUCTION

While primary production studies have been conducted in great numbers in the marine environment (Yentsch, 1963; Raymont, 1966; Parsons and Takahashi, 1973), less attention has been devoted to the determination of secondary production in benthic marine invertebrates (Mann, 1969; Waters, 1977).

Numerous researchers agree that measurement of benthic production is essential to the formulation of a dynamic concept of an ecosystem (Clarke, 1946; Hughes, 1970a and 1970b; Borkowski, 1974; Burke and Mann, 1974). Reviewing the importance of benthic organisms in marine ecosystems, Mills (1975) specifically points to the need for such benthic marine production studies.

Because shallow estuaries are extremely important feeding and nursery areas for many species, which may be important either economically or ecologically (De la Cruz, 1973; Nixon and Oviatt, 1973; Oviatt and Nixon, 1973; Gosselink et al., 1974), production studies in these areas are especially desired (Warwick and Price, 1975). In addition, Rhoads et al. (1978) indicate that data on rates of seasonal colonization and production would be very useful in managing dredge disposal in marine environments.

Hedgepeth (1957, p. 722) indicates that oysters and mussels form important reef-like aggregations in estuaries. Perceiving this, several researchers have initiated production or production related studies on these organisms (Kuenzler, 1961; Galstoff, 1964;

Dame, 1972; Wolff and de Wolf, 1977).

Production investigations involving infaunal bivalves have been conducted on the soft clam, Mya arenaria (Munch-Petersen, 1973), and on Macoma balthica (Green, 1973; Warwick and Price, 1975). Hibbert (1977a, 1977b) has recently completed a detailed production investigation on the hard clam, Mercenaria mercenaria. Still, many species have not been investigated.

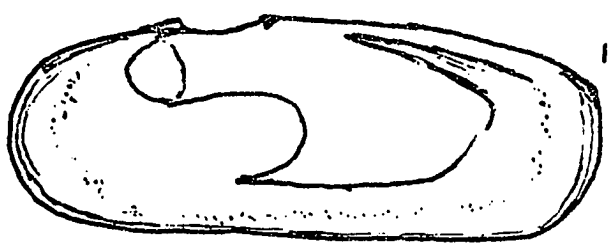
In contrast to estimations of biomass or numbers of individuals, which are frequently made on the basis of one or two large field studies, production studies require a planned series of field collections taken at several intervals throughout the year. The resulting data are analyzed for variations in the number of individuals and biomass during that period. This usually allows the investigator to discern the dynamics of the population in terms of production, biomass, and growth.

In conjunction with this lack of basic data on benthic production in estuarine invertebrates, Chanley and Castagna (1971) have noted that, while the stout razor clam, Tagelus plebeius (Figure 1) probably makes up more of the biomass in the estuaries and lagoons of Virginia than any other bivalve, little is known about the biology of the species. This may be due to its lack of major economic importance. The fact that Tagelus plebeius is a deep burrower, often found 40 to 50 cm below the sediment surface (Pearse et al., 1942; Dauer et al., 1979), has probably discouraged detailed studies.

With great difficulty, Chanley and Castagna (1971) induced Tagelus plebeius to spawn in the laboratory and described the early

Figure 1. *Tagelus plebeius* shell.

EXTERIOR



INTERIOR

50 mm

larval development. Tagelus plebeius is still categorized (Chanley, 1975) with those marine bivalves which are difficult or impossible to spawn under laboratory conditions.

The internal anatomy of Tagelus plebeius was described by Blommer (1907), while Allen (1954) reported the general distribution in mud and sand environments of Maryland. In a South Carolina salt marsh study, Holland and Dean (1977a and 1977b) reported the general intertidal distribution in relation to sediment characteristics and determined the age structure of the population in that area. Tagelus plebeius is also found abundantly in shallow subtidal areas (Pfitzenmeyer, 1961; Wass, 1972), at water depths of one to two meters.

No study has been conducted to determine the annual production of this abundant, deep-burrowing bivalve. Holland and Dean (1977b) suggest that such a study will be necessary for this and other deep-burrowing benthic organisms before their role in the energetics of estuarine environments can be determined.

Thus, the basic need and desire for more field data in order to determine benthic invertebrate production, especially for studies on abundant, deep-burrowing invertebrates such as Tagelus plebeius, has been established.

OBJECTIVES OF THE STUDY

The objectives of this dissertation were threefold. The first objective was to estimate the annual production of Tagelus plebeius in the intertidal environment at Lynnhaven Inlet, Virginia. In conjunction with this primary goal, data were gathered and analyzed to estimate growth, life span, and annual fluctuations in density, biomass, sediment properties, temperature, and salinity. The second objective was to permit a comparison of production in various sediment environments by collecting samples from three separate, though closely situated sites. The third objective was to assess the effect of sample interval on the estimate of production for Tagelus plebeius by collecting data at relatively short intervals (approximately six weeks) and then analyzing them as if the intervals were 6, 12, 24, and 52 weeks.

METHODS

Definition of Production

Before production can be determined for any species population, the term production must be defined. This is especially important because the word has acquired many meanings, some of which are not applicable to this study and confuse the situation (Davis, 1963; Waters, 1977).

The measurement of biomass alone is not a measurement of production (Anderson and Hooper, 1956). Rather, production must be defined in terms of a rate. Because many benthic invertebrates have a life span of one year or more, production may be defined best in terms of a unit weight, per unit of bottom area, per year (Crisp, 1971).

Thorson (1957, p. 491) defines production as follows:

> By "production" we understand the sum of organic matter produced by living organisms in a given area or volume and a given time, inclusive of such organisms, which in the given time might have developed and disappeared. Or, production is the total quantity of organisms formed in a given area or volume during a definite period of time, with no relation to their further destiny.

This meaning has been supported by other researchers (Clarke, 1946; Clarke et al., 1946; Hayne and Ball, 1956; Peer, 1970; Maitland and Hudspith, 1974). It is also the accepted definition of the International Biological Programme (Crisp, 1971; Winberg et al., 1971). As such, it will be the accepted definition for this study.

However, it should be understood that secondary production, as

defined above, is really net secondary production as respiratory energy is not included. Note that Thorson's definition ignores respiration. The usual convention in the benthic secondary production literature is to use the word production in place of net secondary production (Mann, 1969; Waters, 1977).

Production Equations

A numerical method for calculating production must be outlined. The general method can then be modified for specific investigations. As it clarifies the need for certain field data, the derivation of the production equation used in the present study is given below. For a more thorough discussion of the methodology, refer to Crisp (1971), Winberg (1971), and Winberg et al. (1971).

Annual production is first determined for each cohort (year-class) present. These values are summed to give the total production for the population. In the secondary production literature this is usually referred to as the method of Crisp (1971).

In species with life spans of one year or less, this procedure is fairly simple. Only one or two year-classes are present at a given time. However, if the species of interest has a life span of several years, some method must be found to separate the year-classes for production analysis.

In the most unusual case where no mortality is present, the number of individuals in a year-class at the beginning (N_o) and at the end (N_t) of a time interval (t), will be the same.

With growth over the interval t, the average weight of an

individual in the year-class at the end of the time interval ($\bar{w}_t$) will be greater than the average weight of an individual at the beginning of the time interval ($\bar{w}_o$). Production (P) may be computed in this case by taking the difference between the final biomass (B_t), where $B_t = \bar{w}_t N_t$, and the initial biomass (B_o), where $B_o = \bar{w}_o N_o$

$$P = (B_t - B_o) = \bar{w}_t N_t - \bar{w}_o N_o \quad (1)$$

Zero mortality populations do not exist, except over very short time intervals. Growth of individuals occurs concurrently with elimination (loss of individuals due to predation or death by any cause). If in fact the population does have the same biomass at the end of a time interval as at the beginning, then production has been exactly matched by elimination (B_e)

$$P = B_e \text{ only if } B_o = B_t \quad (2)$$

However, if $B_o \neq B_t$, and $N_o > N_t$, then

$$P = B_e + (B_t - B_o) \quad (3)$$

Values of production over some time intervals may be negative or positive. Negative values have been associated with long periods of reduced feeding (Warwick and Price, 1975; Warwick et al., 1978) when there is a loss of individual weight, $\bar{w}_o > \bar{w}_t$ (Wolff and de Wolf, 1977).

Equation (3) is suitable for production determination if B_e can be determined. From Thorson's (1957) definition, this is the biomass of the living organisms "...which in the given time might have developed and disappeared."

If elimination is considered in terms of the number of individuals lost from the population in a given time, elimination (N_e) is defined by

$$N_e = (N_o - N_t) \tag{4}$$

Elimination in terms of biomass, is equal to $(N_o - N_t)$ multiplied by the mean weight of the individuals in the same period of time ($\bar{w}$)

$$B_e = \bar{w}(N_o - N_t) \tag{5}$$

Substituting the terms of B_e from equation (5) back into equation (3), production for the period t, is

$$P = (N_o - N_t)\,\bar{w} + (B_t - B_o) \tag{6}$$

If the interval between observations is short, then $\bar{w}$ is approximated by

$$\bar{w} = \tfrac{1}{2}(\bar{w}_o + \bar{w}_t) \tag{7}$$

Substituting the terms of $\bar{w}$ from equation (7) back into equation (6) yields

$$P = \tfrac{1}{2}(\bar{w}_o + \bar{w}_t)(N_o - N_t) + (B_t - B_o) \tag{8}$$

Finally, substituting the terms of B_o and B_t into equation (8) yields a definition of production over the time interval t, as

$$P = \tfrac{1}{2}(\bar{w}_o + \bar{w}_t)(N_o - N_t) + (\bar{w}_t N_t - \bar{w}_o N_o) \tag{9}$$

which reduces to

$$P = \frac{N_t + N_o}{2} (\bar{w}_t - \bar{w}_o) \qquad (10)$$

This will give the value of production for one particular year-class over one time interval, t. Naturally, to obtain production over all the time intervals, the equation must be written as

$$P = \sum_{t=0}^{n} \frac{N_t + N_c}{2} (\bar{w}_t - \bar{w}_o) \qquad (11)$$

The method does not allow the determination of the production resulting from mucus, spawn, or dissolved organic materials. The calculation is carried out for each year-class present, then the values for all year-classes are summed to give annual production. The method assumes no immigration or emigration in the juvenile and adult populations. Though migration has been reported for some species of razor clams (Williams and Porter, 1971), none has been reported for Tagelus plebeius by Holland and Dean (1977a and 1977b) or observed in the present study.

In selecting an appropriate sampling interval, Winberg (1971) indicates that while monthly collections are usually required for species which live for only one year, those organisms with life spans longer than one year usually may be analyzed for production using three to five collections during the year. The sampling interval is also tempered by the resources available for the project, the overall scope of the study, and the a priori information available to the researcher concerning the life cycle of the species in question.

In other studies of annual production in benthic marine

bivalves the number of collections have ranged from six to twelve per year. Milne and Dunnet (1972) used six collections to determine the production of Mytilus edulis. Arntz (1971), studying subtidal bivalves, sampled every two months. The same procedure was followed by Buchanan and Warwick (1974) in a production study on bivalves. Ansell and Trevallion (1968), Hughes (1970b), and Burke and Mann (1974), sampled every month while studying Tellina tenuis, Scrobicularia plana, and Mya arenaria, respectively.

Field Study

From an intertidal sand flat (Figure 2) in Lynnhaven Inlet, Virginia, samples were taken at three main sites (20m by 20m) at about six week intervals between December 1977 and December 1978. The main sites were approximately 50 m apart and were selected in an area where Tagelus plebeius had been found in a previous investigation. Wooden stakes were driven into the sediment to mark the four corners of each main site during the study.

Since a quantitative collection method was necessary for the study, a flushing-coring device similar to one described by Van Arkel and Mulder (1975), was utilized (Figure 3). The device was designed for: (1) sampling a constant portion (0.02 m^2) of the bottom, (2) sampling to a depth greater than 30 cm in coarse sand or soft mud, and (3) sampling in water with a depth of up to 2.5 m.

While in operation, water was pumped into the space between two concentric polyvinychloride (PVC) tubes. The flushing-corer was forced down into the sediment to a depth of 65 to 70 cm. Water

Figure 2. Field study area at Lynnhaven Inlet, Virginia.

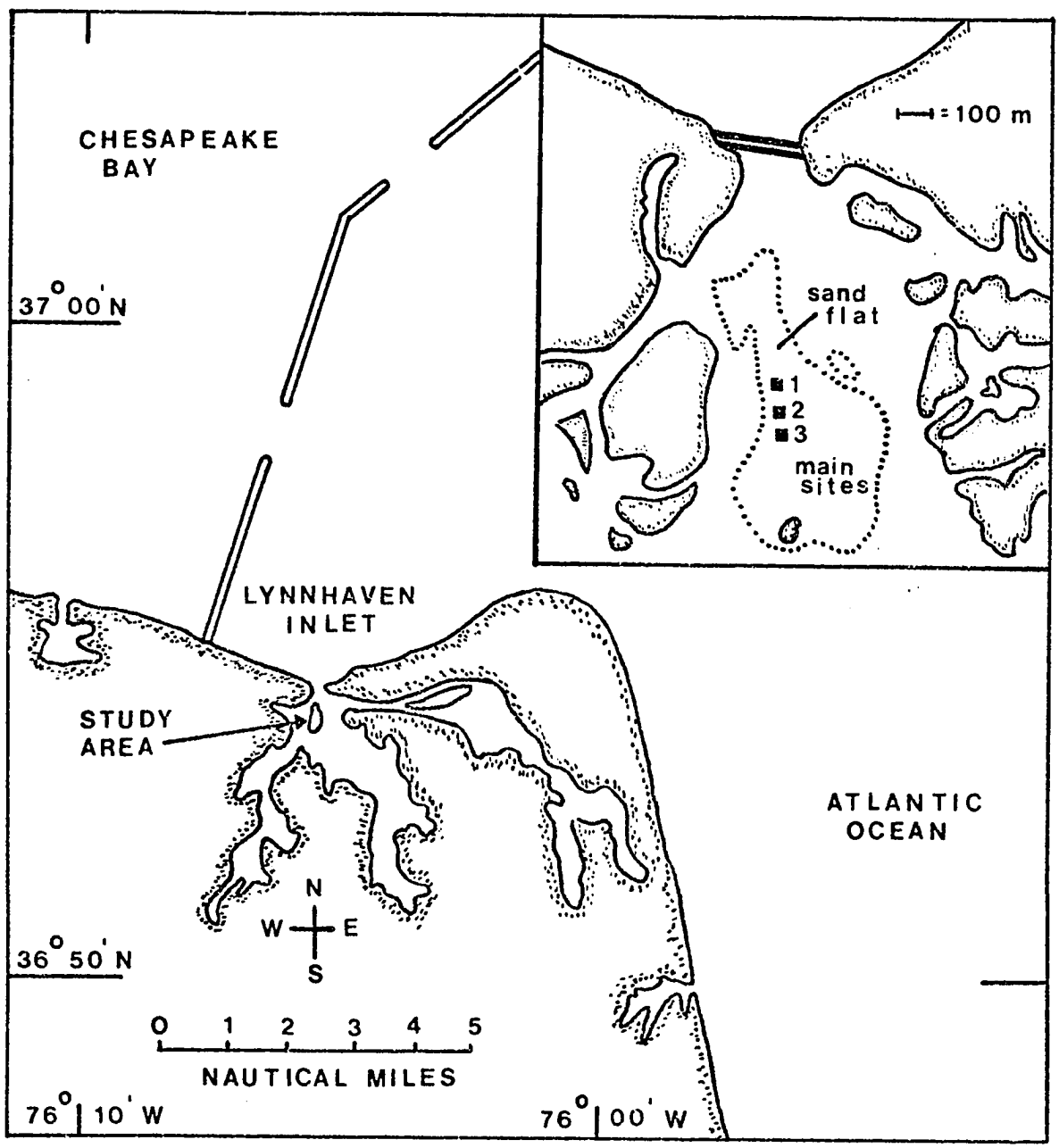
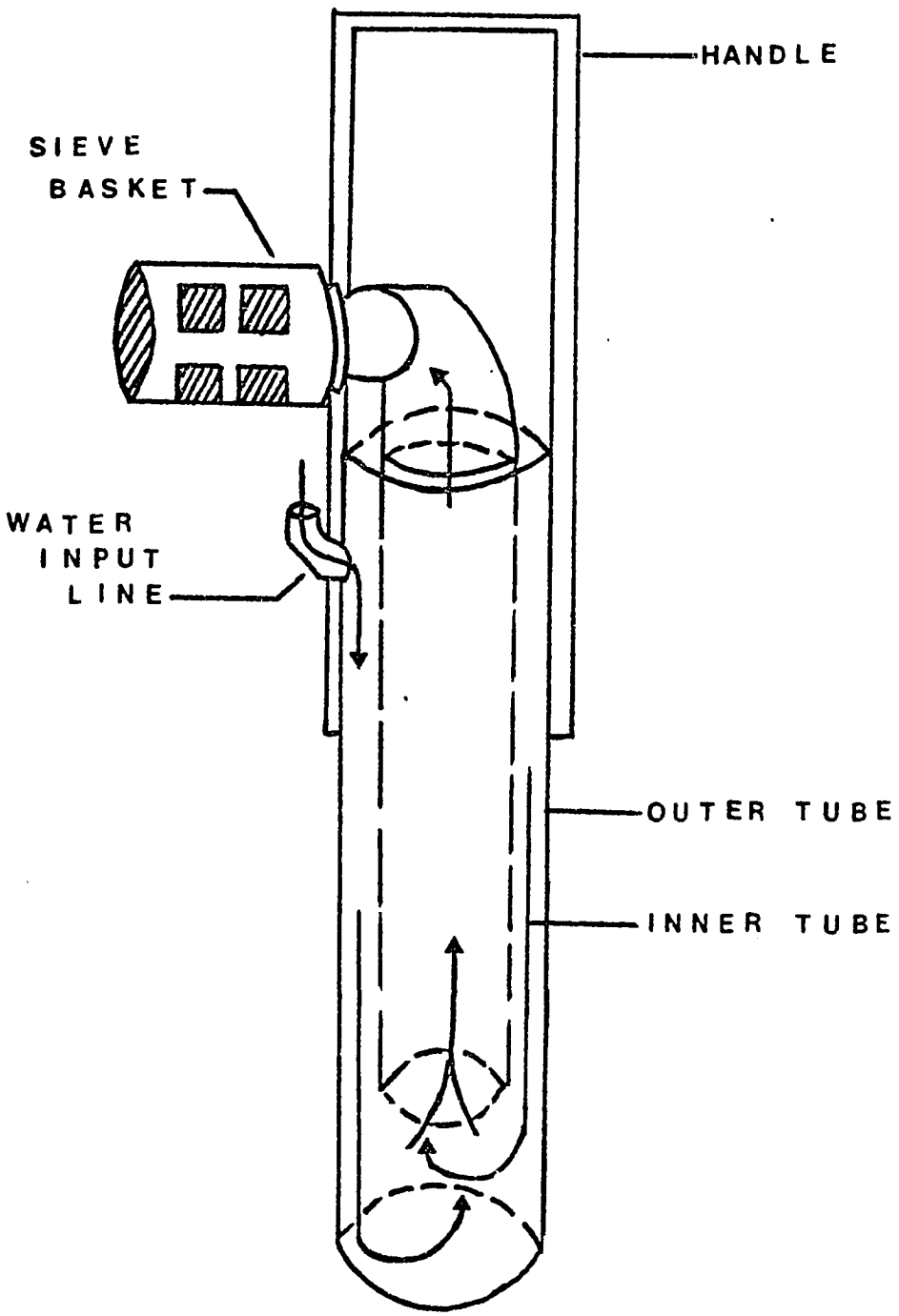


Figure 3. Flushing-coring sampler. Arrows indicate direction of water flow.



turbulence within the tube created a suspension of sediment and all associated organisms which were forced up the inner PVC tube and through the attached sieve basket. No water or sediment escaped from the outer PVC tube while sampling. The device was effective not only in raising large specimens of Tagelus plebeius, but also large specimens of Mercenaria mercenaria and Mya arenaria. A wire screen of 2.5 mm was used on the removable screen bucket attached to the device.

During each collection period, five subsites (2.0 m by 1.5 m) were selected within each major site using numbers drawn from a random numbers table and a square grid system. Wooden stakes were used to mark the subsites and to ensure that no area was sampled twice during the study. At each subsite fifteen cores were taken and pooled as a single sample (0.3 m^2). Thus, 1.5 m^2 of bottom area was sampled at each major site. The bivalves were kept on ice in the field, then placed into heavy duty freezer bags and frozen in the laboratory prior to analysis.

Temperature and salinity were determined at each site with an immersion thermometer and a refractometer, respectively.

Two sediment samples were collected from each subsite. A small PVC coring tube was pressed 10 cm into the sediment to collect the samples. The sediments were stored in small glass jars. The depth of the redox-potential-discontinuity (RPD) was estimated visually in the field at each subsite. At this depth, reducing conditions replace the oxidizing conditions found in the sediments above. A change in sediment color marks the RPD (Fenchel and Riedl, 1970).

Laboratory Procedures

All specimens of Tagelus plebeius were counted and the total shell length (S_L) was measured. This was considered to be the maximum anterior to posterior distance measured on the shell. The flesh of all unbroken specimens was extracted from the shell and the biomass of each determined individually. The flesh was dried at 60°C (Crisp, 1971) for three to five days, then ashed in a muffle furnace at 500 to 550°C for four hours. The weight loss during incineration represents ash-free dry weight (AFDW). This was used as a measure of biomass throughout the study.

Clearly distinguishable annual growth rings on the shells have been used to separate year-classes in some species (Haskin, 1954; Wilbur and Owen, 1964; Negus, 1966; Lammens, 1967). This, however, was not possible with the Lynnhaven Inlet specimens of Tagelus plebeius; year-classes were separated in the present study using the probability paper methods suggested by Harding (1949) and Cassie (1954).

The S_L and AFDW data were used to compute regression equations (AFDW as the dependent variable) for each site and sample date of the study. These equations were subsequently used to determine the AFDW of the average size clam from each year-class at each site. The information was then substituted into equation (11) to determine production.

Maximum life span and size were estimated for each site with a Ford-Walford growth plot (Walford, 1946; Hancock, 1965).

The organic content of the sediment was determined by drying a

small sample (15 g) for one to two days at 100°C, then ashing in a muffle furnace at 500 to 550°C for two hours. The weight loss on incineration was considered to be the organic content and was recorded as a percentage.

Mean grain size (Mz), median grain size (M_d), and sorting coefficients (σ_I) were determined according to Folk (1974). Sediments were wet sieved at 4.0 ϕ (0.0625 mm) to remove the silt-clay fraction (phi unit = $\phi = \log_2$ grain diameter in millimeters). The sand fraction was air dried, then sieved through a series of 11 Wentworth sieves at $\frac{1}{2}$ ϕ intervals from -1.0 ϕ to 4.0 ϕ.

The pan fraction (smaller than 4.0 ϕ) was added to the weight of the dried silt-clay fraction and assigned to the 5.0 ϕ size. The weights of the sediment on each sieve were used as input data in the FORTRAN IV program, developed by Darby and Wobus (1976). The program computed Mz, Md, σ_I, and the silt-clay percentage.

Statistics

Means, standard deviations, standard errors, linear regressions, correlations, and Kruskal-Wallis one way analysis of variance tests were computed with the SPSS programs (Nie et al., 1975), while analysis of covariance tests were computed with BMDP programs (Dixon, 1975). All SPSS and BMDP programs were used on the Old Dominion University, Dec-10 computer.

RESULTS

Bivalve Abundance and Environmental Variables

Means and standard errors are summarized by site in Table 1 for all bivalve densities, sediment variables, temperature, and salinity. Tagelus plebeius, Mya arenaria, and Mercenaria mercenaria were the only bivalves found. The mud snail, Nassarius obsoletus was found on occasion. Sampling for this gastropod was not quantitative as the snails were attracted to organic material stirred up by the sampling device; therefore, counts were not made on the snails collected.

The variables in Table 1 were tested by the nonparametric Kruskal-Wallis analysis of variance (Siegel, 1956; Conover, 1971) for significant differences due to site and also for significant differences due to seasonal change at each site (Table 2). The density of Mercenaria mercenaria, silt-clay percentage, organic percentage, temperature, and salinity showed no significant differences between sites.

Figure 4 shows the change in abundance of Tagelus plebeius at each site over the sampling year. Tagelus plebeius was significantly more abundant at site 2 than at site 1 ($p < 0.05$) or site 3 ($p < 0.01$).

Figure 5 shows the change in temperature and salinity during the sampling year.

The organic percentage of the sediment was always low at all

Table 1. Summary statistics for biological and physical data collected between December 1977 and December 1978 at Lynnhaven Inlet, Virginia.

Variable	Site 1		Site 2		Site 3	
	Mean	SE	Mean	SE	Mean	SE
All Bivalves (No. m^{-2})	47.3	4.0	60.4	3.9	42.7	2.7
Tagelus plebeius (No. m^{-2})	22.6	3.0	47.9	3.3	39.0	2.6
Mya arenaria (No. m^{-2})	24.1	2.7	11.9	1.7	2.1	0.5
Mercenaria mercenaria (No. m^{-2})	0.6	0.2	0.5	0.2	1.5	0.3
RPD (cm)	1.8	0.2	0.6	0.1	0.5	0.0
Silts-clays (%)	2.72	0.15	2.82	0.14	2.81	0.17
Organic content (%)	0.53	0.03	0.55	0.04	0.53	0.03
Mz (ø)	2.19	0.03	2.10	0.02	1.93	0.03
M_d (ø)	2.31	0.02	2.25	0.03	1.98	0.04
σ_I (ø)	0.80	0.02	0.88	0.01	0.87	0.01
Temperature (°C)	14.1	1.2	13.9	1.2	14.3	1.2
Salinity (°/oo)	16.9	0.5	17.2	0.4	17.3	0.5

Table 2. Biological and physical variables tested for significant differences due to site and seasonal variations at each site. H is the statistic of the Kruskal-Wallis analysis of variance.

Variable	Between sites	Between seasons at		
		Site 1	Site 2	Site 3
	H	H	H	H
All Bivalves (No. m^{-2})	11.7**	7.6	13.3	15.8*
Tagelus plebeius (No. m^{-2})	34.2**	3.9	8.7	12.1
Mya arenaria (No. m^{-2})	64.0**	3.7	13.5	20.0*
Mercenaria mercenaria (No. m^{-2})	4.9	3.1	1.1	5.8
RPD (cm)	49.7**	27.6**	21.8**	12.6
Silts-clays (%)	0.7	17.1	24.4**	25.4**
Organic content (%)	0.1	21.1**	27.5**	28.2**
Mz (ø)	33.0**	28.2**	3.7	5.4
M_d (ø)	39.0**	21.9**	5.4	4.2
σ_I (ø)	10.1**	31.4**	3.0	1.4
Temperature (°C)	0.3	-[a]	-	-
Salinity (°/oo)	0.2	-[a]	-	-

* $p < 0.05$
** $p < 0.01$
[a]Dashes indicate insufficient data for the test.

Figure 4. The density (No. m^{-2}) of *Tagelus plebeius* at each site during the sampling year (± 1 standard error).

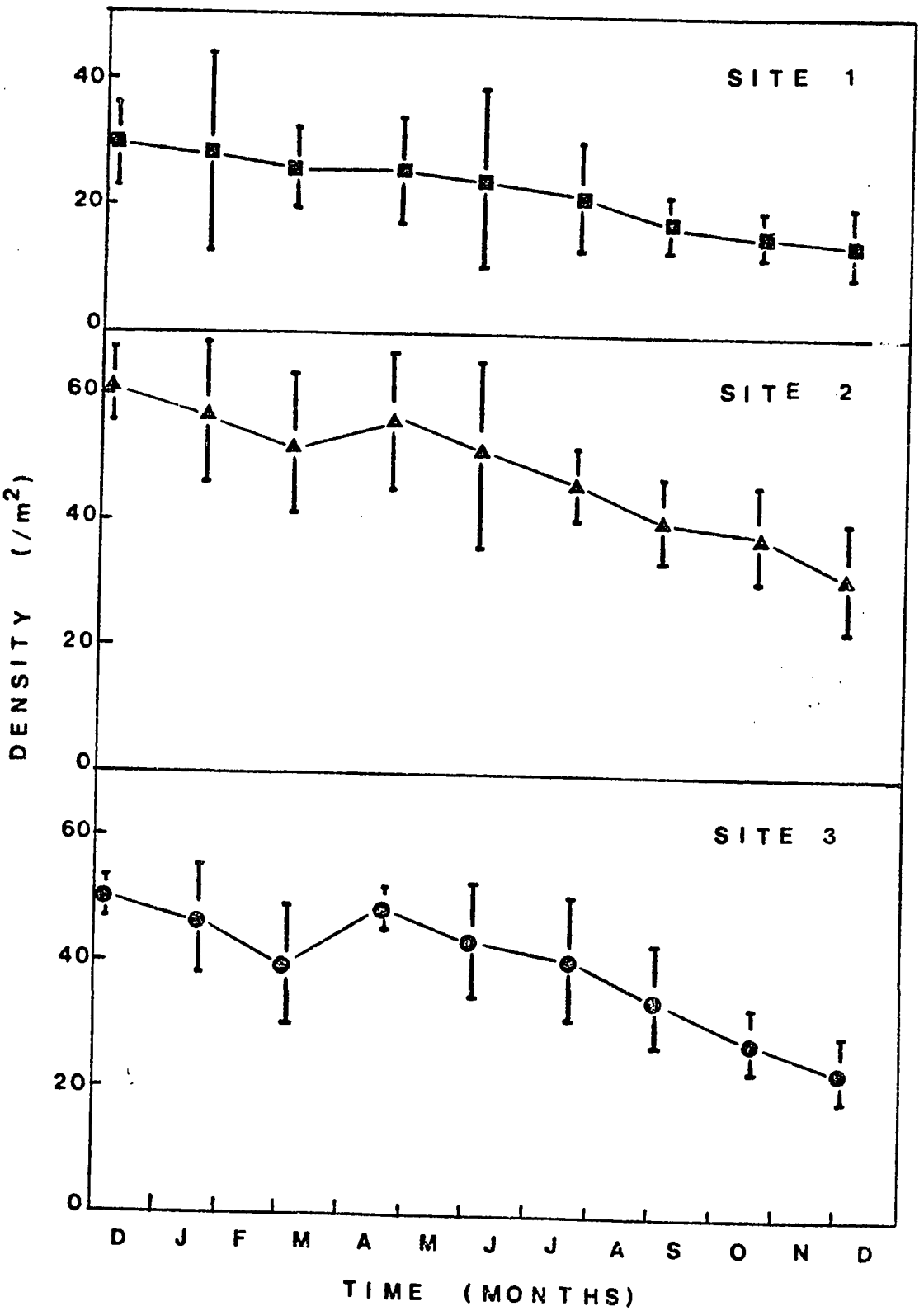
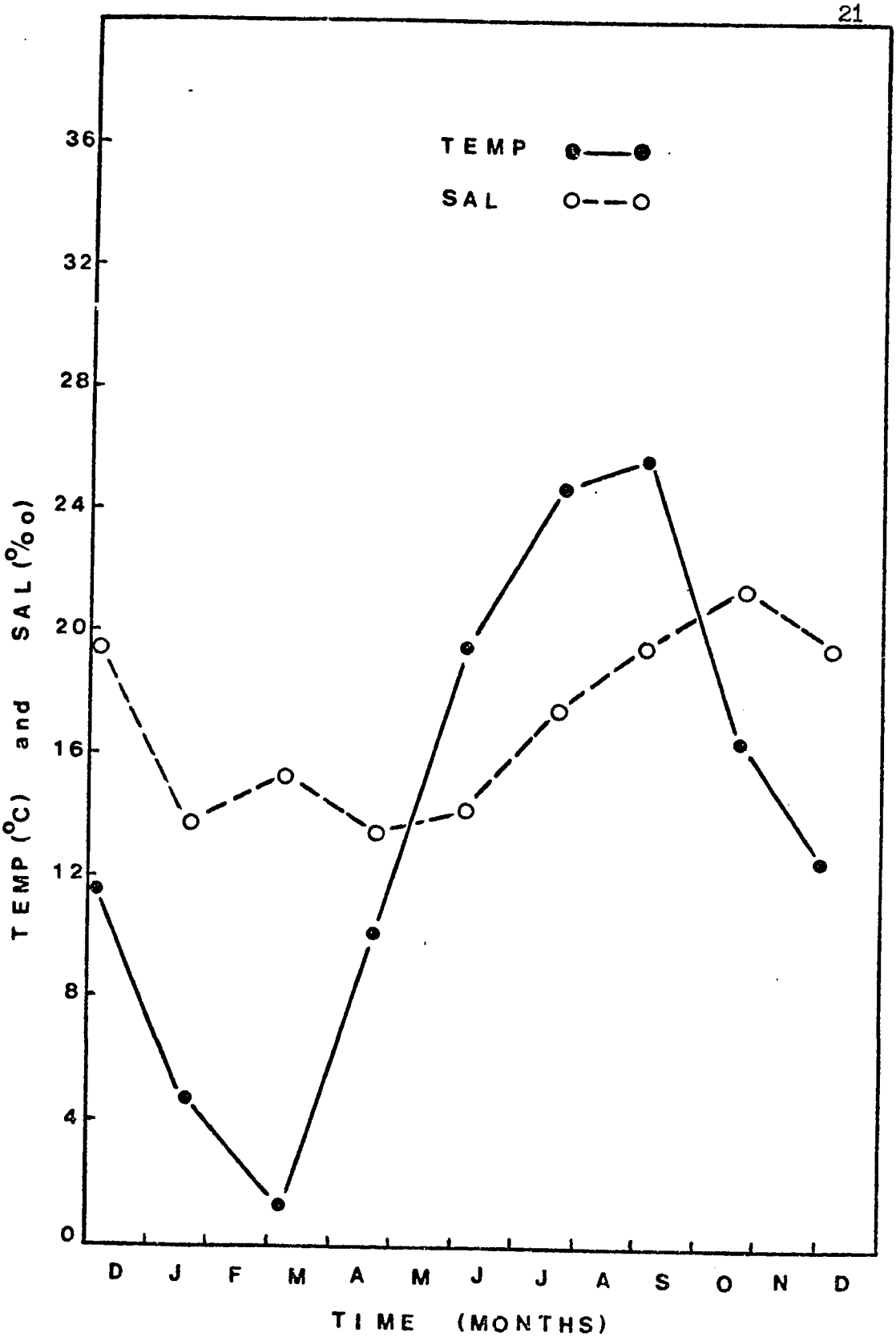


Figure 5. Mean values of temperature (^{o}C) and salinity ($^{o}/oo$) at the sites during the sampling year. Each point represents the mean of three numbers, one from each site.



sites, averaging about 0.5%. The silt-clay percentage was usually less than 3% at all sites. The sediments at sites 1 and 2 were composed of fine, moderately-sorted sand, while those at site 3 were composed of medium, moderately-sorted sand (Folk, 1974).

The Spearman rank correlation analysis showed no significant correlation between the separate abundances of Tagelus plebeius, Mya arenaria, or Mercenaria mercenaria, and any of the sediment variables. However, at site 2 there was a significant correlation between Mya arenaria abundance and salinity ($r_s = -0.392$, $p < 0.01$). At site 3 there were significant correlations between Tagelus plebeius abundance and salinity ($r_s = -0.350$, $p < 0.05$), and between Mya arenaria abundance and salinity ($r_s = -0.356$, $p < 0.05$).

When correlating the abundance of all clams as a group with the other variables, results were similar. At site 1 the total clam abundance correlated significantly with salinity ($r_s = -0.328$, $p < 0.05$) and with the sorting coefficient ($r_s = 0.336$, $p < 0.05$); at site 2 with salinity ($r_s = -0.311$, p 0.05) and the silt-clay percentage ($r_s = 0.315$, $p < 0.05$); and at site 3 with salinity ($r_s = 0.336$, $p < 0.05$).

Age Composition

The age composition of the Tagelus plebeius population for each site and sampling date is shown in Table 3. The 1978 year-class juveniles were first collected in April. Recruitment was low at site 1 (2.9 m^{-2}) but heavier at sites 2 (10.9 m^{-2}) and 3 (12.2 m^{-2}).

Bimodal recruitment occured in 1977 at all sites. The spring

Table 3. Age composition (number per square meter) of Tagelus plebeius on each sample date.

Site	Year-class	Date (1977-1978) Dec. 3-5	Jan. 18-20	Mar. 4-6	Apr. 18-21	June 3-5	July 18-21	Sept. 2-4	Oct. 18-20	Dec. 3-5
1	1978	0.0	0.0	0.0	2.9	3.3	2.1	1.5	1.4	1.5
1	1977-late	5.1	5.1	4.3	4.1	3.3	3.6	2.8	1.4	1.5
1	1977-early	5.1	3.9	4.8	4.0	3.6	3.6	3.5	2.7	2.8
1	1976	16.5	16.8	14.6	13.4	12.7	11.3	10.8	9.8	8.9
1	1975	3.3	2.3	1.7	1.5	1.2	1.0	0.0	0.0	0.0
2	1978	0.0	0.0	0.0	10.9	9.7	9.0	8.4	7.5	5.6
2	1977-late	8.3	7.9	7.7	6.1	6.1	5.7	4.0	3.7	2.7
2	1977-early	17.5	16.3	14.9	14.3	11.8	11.1	10.4	9.3	7.7
2	1976	26.4	25.5	23.6	21.0	22.1	19.7	17.2	16.8	16.0
2	1975	9.2	6.5	5.1	3.7	1.5	0.6	0.0	0.0	0.0
3	1978	0.0	0.0	0.0	12.2	11.7	11.6	10.2	8.4	7.3
3	1977-late	11.9	11.5	10.2	9.0	8.7	8.4	6.1	5.1	2.9
3	1977-early	9.9	9.2	8.3	8.0	7.8	6.8	4.4	4.5	2.7
3	1976	18.7	18.4	16.5	16.1	13.0	12.6	13.3	10.1	9.7
3	1975	8.9	6.9	4.3	3.4	2.2	0.6	0.0	0.0	0.0

recruitment in that year (1977-early year-class) is in agreement with data presented by Holland and Dean (1977b). They report no bimodal recruitment for Tagelus plebeius studied in a South Carolina salt marsh, even though two out-of-phase juveniles were collected during their three year study.

The 1976 year-class was the most abundant at all sites throughout the year. The oldest year-class (1975) was absent on the sand flat after the July sampling.

The number of clams in each year-class was tested (Kruskal-Wallis test) to delineate significant differences between sites. The 1978 year-class was significantly more abundant at sites 3 ($p < 0.01$) and 2 ($p < 0.05$) than at site 1. The 1977-late year-class was significantly more abundant ($p < 0.01$) at site 3 than at site 1. Both the 1977-early and the 1976 year-classes at site 2 were significantly more abundant than at sites 3 ($p < 0.05$) and 1 ($p < 0.01$). No significant differences in abundance were found in the 1975 year-class between sites.

In general, the younger year-classes (1978, 1977-late) were more abundant at site 3, while the older year-classes (1977-early, 1976) were more abundant at site 2.

Size Composition

The S_Ls for each year-class of Tagelus plebeius at each site are shown in Table 4. These S_Ls correspond to the age composition data in Table 3.

In the 1978 year-class, the juveniles grew rapidly at all sites

Table 4. Size composition (average shell length in millimeters) of the Tagelus plebeius population on each sample date.

Site	Year-class	Date (1977-1978) Dec. 3-5	Jan. 18-20	Mar. 4-6	Apr. 18-21	June 3-5	July 18-21	Sept. 2-4	Oct. 18-20	Dec. 3-5
1	1978	-[a]	-	-	19.9	29.2	36.9	43.9	50.0	56.2
1	1977-late	26.0	27.6	38.3	46.3	52.0	56.9	61.2	61.2	63.9
1	1977-early	54.3	53.1	62.7	64.7	66.8	72.7	70.1	73.0	74.3
1	1976	67.1	68.6	73.7	73.9	76.2	76.3	79.4	79.6	83.0
1	1975	80.2	84.7	84.8	82.2	86.6	87.4	-	-	-
2	1978	-	-	-	21.0	28.5	37.9	43.5	49.5	54.9
2	1977-late	22.0	26.6	38.6	49.2	53.9	57.8	61.0	62.3	63.1
2	1977-early	55.4	57.2	60.9	65.0	65.3	70.3	71.5	72.9	73.2
2	1976	72.4	71.8	71.7	74.8	76.1	77.1	78.4	78.5	82.7
2	1975	84.2	84.2	84.1	84.3	84.7	88.3	-	-	-
3	1978	-	-	-	20.7	29.8	35.7	42.9	48.7	51.5
3	1977-late	27.7	28.0	37.2	47.2	51.8	56.3	60.9	61.9	63.2
3	1977-early	57.5	53.1	61.0	64.3	65.8	71.1	70.8	73.1	74.6
3	1976	68.0	71.0	73.1	73.8	76.8	77.1	78.2	78.3	82.3
3	1975	84.4	83.3	84.6	84.6	86.2	88.1	-	-	-

[a]Dashes indicate no specimens present.

from about 20 mm, when first sampled in April, to about 53 mm at the beginning of winter. Thus, more than 50% of the total shell growth was completed prior to the start of the first winter.

By comparing the two December sampling periods, it is clear that the bimodal settlement observed in 1977 did not repeat in 1978. The S_Ls in each year-class were tested to determine if the sizes were significantly different between sites (Kruskal-Wallis test). No significant differences were found.

Growth

A Ford-Walford plot of the initial shell length ($S_{L\ t}$) against the shell length after one year ($S_{L\ t+1}$) is shown for Tagelus plebeius in Figure 6. The mean S_Ls from the July sample were used in the linear regression equations (Table 5). The maximum S_Ls were estimated from the intercepts of the regression lines with the no growth line ($S_{L\ t+1} = S_{L\ t}$).

The Ford-Walford plots are a good representation of growth rates actually observed in the study (Table 4). Only two specimens larger than 90 mm were found (91.3 and 91.5 mm, at site 3). No significant difference was found in the slopes or intercepts of the three lines (analysis of covariance).

Shell Length to Body Weight Regressions

The regression of AFDW on S_L was calculated for Tagelus plebeius for each site and sampling date (Table 6). At each site the equations were tested (analysis of covariance) to delineate

Figure 6. Ford-Walford plot of the average initial shell length ($S_{L\ t}$) against the shell length after one year of growth ($S_{L\ t+1}$). The intercept on the $S_{L\ t+1}$ axis is an estimate of the size after one year of growth, while the intercept on the no growth line is an estimate of maximum S_L at each site.

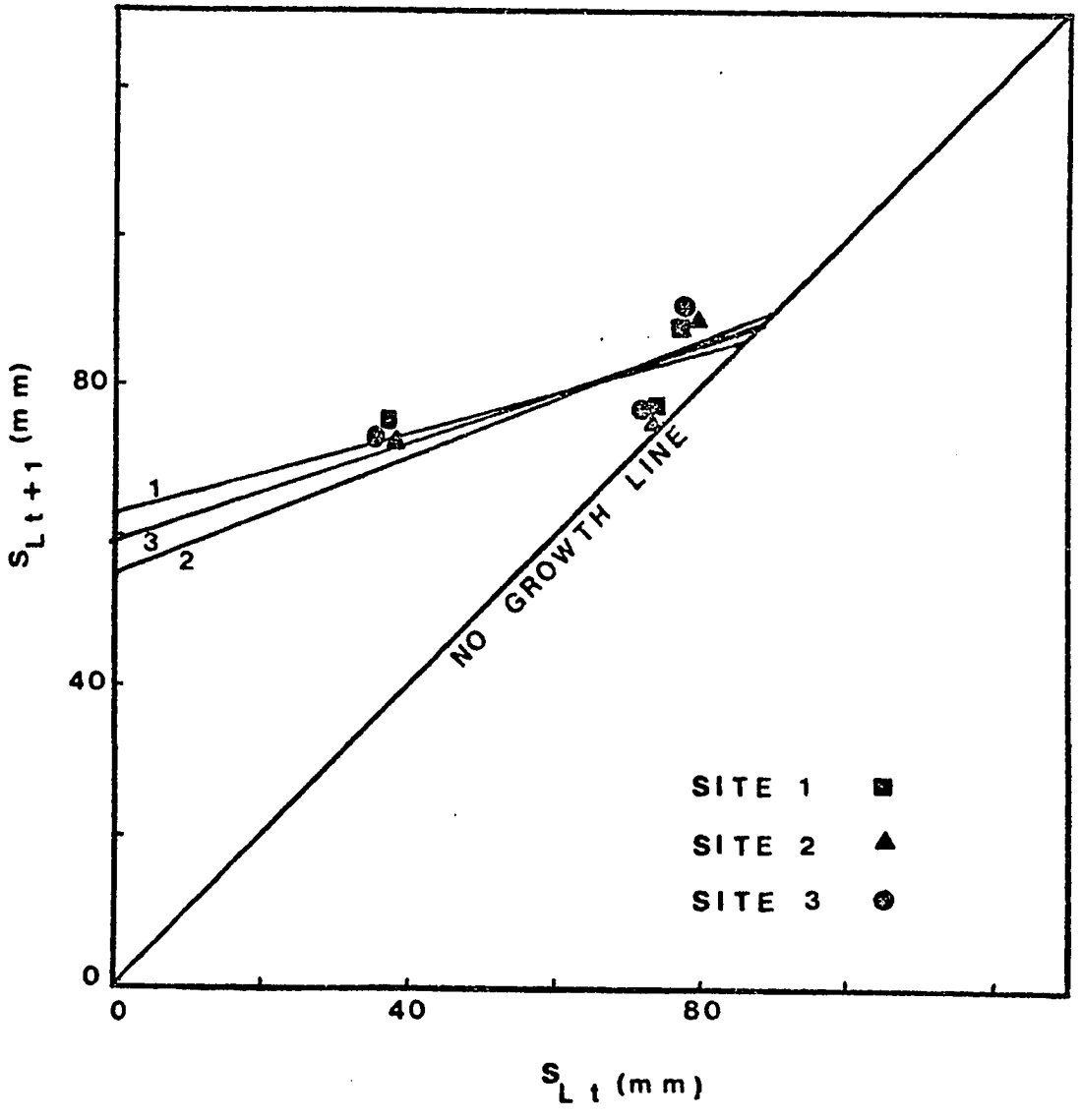


Table 5. The values of terms in the Ford-Walford linear regression $S_{L\ t+1}(mm) = a + b\ S_{L\ t}(mm)$ for Tagelus plebeius. Maximum S_Ls are estimated from the equations.

Site	No. of points	a (intercept)	b (slope)	r (correlation coefficient)	S_L (maximum)
1	3	62.5	0.26	0.75	84.5
2	3	55.1	0.38	0.88	88.9
3	3	58.7	0.33	0.85	87.6

Table 6. The values of terms in the linear regression $\log_{10}$(AFDW in mg) = a + b $\log_{10}$(S_L in mm) for Tagelus plebeius.

Date	Site	No. of clams	a (intercept)	b (slope)	r^2 (coefficient of determination)
Dec. 3-5	1	41	-2.4480	3.0170	0.98
Dec. 3-5	2	86	-2.3422	2.9442	0.97
Dec. 3-5	3	65	-2.2290	2.8863	0.98
Jan. 18-20	1	39	-2.3747	2.9492	0.98
Jan. 18-20	2	69	-1.8848	2.6778	0.97
Jan. 18-20	3	55	-2.1752	2.8520	0.98
Mar. 4-6	1	31	-2.9744	3.2888	0.99
Mar. 4-6	2	69	-3.0917	3.3604	0.99
Mar. 4-6	3	54	-3.1640	3.3960	0.99
Apr. 18-21	1	33	-3.3753	3.5008	0.99
Apr. 18-21	2	68	-3.3093	3.4539	0.96
Apr. 18-21	3	60	-3.3668	3.4898	0.99
June 3-5	1	30	-2.2953	2.9453	0.98
June 3-5	2	64	-2.5553	3.0860	0.99
June 3-5	3	54	-2.4709	3.0371	0.99
July 18-21	1	27	-2.7026	3.1447	0.98
July 18-21	2	58	-2.8893	3.2314	0.99
July 18-21	3	51	-2.7559	3.1608	0.99
Sept. 2-4	1	28	-2.9000	3.2302	0.98
Sept. 2-4	2	54	-3.5968	3.5906	0.99
Sept. 2-4	3	43	-2.5962	3.0656	0.95

Table 6. (Continued)

Date	Site	No. of clams	a (intercept)	b (slope)	r^2 (coefficient of determination)
Oct. 18-20	1	21	-2.4550	2.9960	0.98
Oct. 18-20	2	52	-3.0357	3.2990	0.99
Oct. 18-20	3	37	-2.3591	2.9328	0.98
Dec. 3-5	1	22	-1.4769	2.4795	0.89
Dec. 3-5	2	48	-1.8367	2.6582	0.92
Dec. 3-5	3	31	-1.8340	2.6403	0.90

significant differences over the year. Significant temporal differences were noted at all sites ($p < 0.001$). Sites were also compared with each other on each of the sampling dates to reveal significant differences between sites. The slopes were significantly different ($p < 0.05$) between the sites in January, September, and October. No significant differences in slope were noted between the sites in December (1977), March, April, June, July, or December (1978). However, the intercepts for the March, July, and December (1978) samples were significantly different ($p < 0.05$).

Each equation was used separately to compute AFDW for each site and sample date. Therefore, the AFDWs estimated by the regression equations reflect the differences in body condition at each site over the sampling year.

Biomass

The biomass of Tagelus plebeius on each sampling date was computed from the regression equations in Table 6 using the mean S_Ls in Table 4. The estimates of AFDW were multiplied by the densities of each year-class in Table 3. The results are shown in Tables 7, 8, and 9.

The major portion of the biomass present throughout the year was contributed by the 1976 year-class. The total biomass at site 2 was significantly greater than at sites 1 (Kruskal-Wallis test, $p < 0.01$) and 3 ($p < 0.05$). No significant seasonal variation was found (Kruskal-Wallis test, $p > 0.05$).

Table 7. The biomass (AFDW in mg m^{-2}) of Tagelus plebeius on each sample date at site number one.

Date (1977-1978)	Biomass (AFDW in mg m^{-2}) of year-classes 1978	1977-late	1977-early	1976	1975	Total
Dec. 3-5	-	337.6	3115.1	19085.6	6537.3	29075.6
Jan. 18-20	-	382.5	2014.0	18463.2	4707.0	25566.7
Mar. 4-6	-	734.4	4146.7	21462.0	3964.2	30307.3
Apr. 18-21	42.7	1170.6	3684.4	19659.1	3194.3	27751.1
June 3-5	346.2	1893.9	4320.4	22461.2	3093.5	32115.2
July 18-21	352.8	2360.5	5101.2	18640.5	2528.6	28983.6
Sept. 2-4	381.6	2083.2	4037.6	18630.0	-	25132.4
Oct. 18-20	604.2	1107.3	3621.5	17035.3	-	22368.3
Dec. 3-5	1090.6	1499.4	4067.8	17015.0	-	23672.8
					Mean annual biomass	27219.2

Table 8. The biomass (AFDW in mg m^{-2}) of Tagelus plebeius on each sample date at site number two.

Date (1977-1978)	Biomass (AFDW in mg m^{-2}) of year-classes 1978	1977-late	1977-early	1976	1975	Total
Dec. 3-5	-	338.6	10816.8	35880.2	19502.2	66537.8
Jan. 18-20	-	673.9	10798.8	31051.4	12125.8	54649.9
Mar. 4-6	-	1337.5	11981.1	32846.5	12132.4	58297.5
Apr. 18-21	197.3	2088.6	12812.8	30563.4	8138.2	53800.3
June 3-5	834.2	3747.2	13103.9	39360.1	3717.4	60762.8
July 18-21	1466.1	3631.5	13313.3	31841.1	1503.2	51755.2
Sept. 2-4	1624.6	2604.0	11975.6	27571.6	-	43775.8
Oct. 18-20	2691.0	2834.9	11965.4	27592.3	-	45083.6
Dec. 3-5	3432.8	2396.0	10140.0	29142.4	-	45111.2
				Mean annual biomass		53308.2

Table 9. The biomass (AFDW in mg m^{-2}) of Tagelus plebeius on each sample date at site number three.

Date (1977-1978)	Biomass (AFDW in mg m^{-2}) of year-classes 1978	1977-late	1977-early	1976	1975	Total
Dec. 3-5	-	1023.4	7007.2	21478.8	19071.8	48581.2
Jan. 18-20	-	1030.4	5111.5	23410.3	13784.8	43337.0
Mar. 4-6	-	1507.6	6577.8	24174.2	10347.1	42606.7
Apr. 18-21	205.0	2686.5	7024.0	22865.2	7777.2	40557.9
June 3-5	1187.6	4733.7	8776.6	23392.2	5621.4	43711.5
July 18-21	1644.9	5028.2	8511.6	20374.2	1478.9	37037.8
Sept. 2-4	2611.2	4571.3	5232.5	21451.6	-	33866.6
Oct. 18-20	3268.4	4010.1	5762.7	15821.7	-	28862.9
Dec. 3-5	3539.8	2414.5	3483.0	16218.4	-	25655.7
				Mean annual biomass		38246.4

Production

The production of each year-class of Tagelus plebeius was calculated separately. Computations for the 1977-late year-class at site 1 are shown in Table 10. The year-class production values were summed to give total annual P at each site (Tables 11, 12, and 13). Though annual P did not differ significantly between sites (Kruskal-Wallis test, $p > 0.05$), significant seasonal variation was present ($p < 0.01$).

The production to biomass ratios (P/B), were similar at all sites. The values were 0.67, 0.54, and 0.66 at sites 1, 2, and 3, respectively.

Annual P, mean annual B, and P/B ratios for separate year-classes are given in Table 14. The relationship between P/B ratio and year-class is displayed in Figure 7. The P/B ratios are large for the young year-classes, contrasting with the small values in the old year-classes. Though a larger percentage of the mean annual B is found in the 1975 year-class than in the 1978 year-class, the annual P is always larger in the 1978 year-class.

To observe the affect of sampling interval on annual P, mean annual B, and P/B ratios, these values were computed as if sampling had taken place at 12, 24, and 52 week intervals. The results are presented in Table 15 with the data previously computed at six week intervals.

At all sites there are only small changes in the values of P, B, and P/B when computed at 12 or 24 week intervals. Comparing the data from the larger sample intervals with the data computed

Table 10. Computation of annual production for the 1977-late year-class at site number one.

Date (1977-1978)	No. (m^{-2}) of clams	Mean shell length (mm)	AFDW (mg)	Change in AFDW since last sample (mg)	Mean no. of clams between samples	P ($mg\ m^{-2}$) between samples
Dec. 3-5	5.1	26.0	66.2	-	-	-
Jan. 18-20	5.1	27.6	75.0	8.8	5.1	44.9
Mar. 4-6	4.3	38.3	170.8	95.8	4.7	450.3
Apr. 18-21	4.1	46.3	285.5	114.7	4.2	481.7
June 3-5	3.3	52.0	573.9	288.4	3.7	1067.1
July 18-21	3.6	56.9	655.7	81.8	3.4	278.1
Sept. 2-4	2.8	61.2	744.0	88.3	3.2	282.6
Oct. 18-20	1.4	61.2	790.9	46.9	2.1	98.5
Dec. 3-5	1.5	63.9	999.6	208.7	1.4	292.2
					Total	2995.4

Table 11. Annual production estimates for all year-classes of *Tagelus plebeius* at site number one.

Date (1977-1978)	Production (mg m^{-2}) between sample dates 1978	1977-late	1977-early	1976	1975	Total
Dec. 3-5	-	-	-	-	-	-
Jan. 18-20	-	44.9	-424.8	-957.8	183.4	-1154.3
Mar. 4-6	-	450.3	1529.0	5824.7	570.8	8374.8
Apr. 18-21	-	481.7	251.7	-40.6	-323.8	369.0
June 3-5	279.3	1067.1	1060.2	3919.5	627.8	6953.9
July 18-21	170.4	278.1	780.8	-1428.0	-54.2	-252.9
Sept. 2-4	155.5	282.6	-948.2	829.4	-	319.3
Oct. 18-20	248.1	98.5	581.9	137.0	-	1065.5
Dec. 3-5	413.7	292.2	312.2	1630.9	-	2649.0
Total ($mg\ m^{-2}$)	1267.0	2995.4	3142.8	9915.1	1004.0	18324.3

Total Production = 18324.3 mg m^{-2} $year^{-1}$

Mean annual biomass = 27219.2 mg m^{-2}

Therefore P/B = 0.67

Table 12. Annual production estimates for all year-classes of *Tagelus plebeius* at site number two.

Date (1977-1978)	Production (mg m^{-2}) between sample dates 1978	1977-late	1977-early	1976	1975	Total
Dec. 3-5	-	-	-	-	-	-
Jan. 18-20	-	360.4	750.4	-3676.4	-1983.5	-4549.1
Mar. 4-6	-	689.5	2209.0	4282.9	2977.7	10159.1
Apr. 18-21	-	1164.0	1341.7	1418.3	-789.4	3134.6
June 3-5	699.4	1658.6	2788.5	7033.0	724.9	12904.4
July 18-21	722.9	134.5	1013.5	-3442.2	27.1	-1544.2
Sept. 2-4	265.4	66.7	-517.3	-244.7	-	-429.9
Oct. 18-20	1323.2	437.8	1324.0	669.8	-	3754.8
Dec. 3-5	1677.7	387.8	257.6	2935.6	-	5258.7
Total ($mg_{m^{-2}}$)	4688.6	4899.3	9167.4	8976.3	956.8	28688.4

Total Production = 28688.4 mg m^{-2} $year^{-1}$

Mean annual biomass = 53308.2 mg m^{-2}

Therefore P/B = 0.54

Table 13. Annual production estimates of all year-classes of *Tagelus plebeius* at site number three.

Date (1977-1978)	Production (mg m^{-2}) between sample dates 1978	1977-late	1977-early	1976	1975	Total
Dec. 3-5	-	-	-	-	-	-
Jan. 18-20	-	42.1	-1461.1	2300.8	-1146.3	-264.5
Mar. 4-6	-	628.6	2084.7	3354.7	2287.6	8355.6
Apr. 18-21	-	1446.7	701.1	-731.9	-451.8	964.1
June 3-5	1016.4	2161.3	1952.3	5536.3	749.8	11416.7
July 18-21	467.5	468.7	923.4	-2334.7	-126.6	-601.7
Sept. 2-4	1244.8	1085.8	-350.0	-53.3	-	1927.3
Oct. 18-20	1237.8	206.6	402.2	-542.9	-	1303.7
Dec. 3-5	747.2	185.2	33.8	1044.4	-	2010.6
Total ($mg_{m^{-2}}$)	4713.7	6225.0	4287.0	8573.4	1312.7	25111.8

Total Production = 25111.8 mg m^{-2} $year^{-1}$

Mean annual biomass = 38246.4 mg m^{-2}

Therefore P/B = 0.66

Table 14. Production (P), mean annual biomass (B), and P/B ratios at each site according to year-class. Values in parentheses represent percentages.

Site	Year-class	P ($mg\ m^{-2}\ yr^{-1}$)	B ($mg\ m^{-2}$)	P/B
1	1978	1267.0 (6.9)	313.1 (1.2)	4.05
1	1977-late	2995.4 (16.3)	1285.5 (4.7)	2.33
1	1977-early	3142.8 (17.2)	3789.9 (13.9)	0.83
1	1976	9915.1 (54.1)	19161.3 (70.4)	0.52
1	1975	1004.0 (5.5)	2669.4 (9.8)	0.38
2	1978	4688.6 (16.3)	1138.4 (2.1)	4.12
2	1977-late	4899.3 (17.1)	2183.6 (4.1)	2.24
2	1977-early	9167.4 (32.0)	11878.6 (22.3)	0.77
2	1976	8976.3 (31.3)	31761.0 (59.6)	0.28
2	1975	956.8 (3.3)	6346.6 (11.9)	0.15
3	1978	4713.7 (18.9)	1384.1 (3.6)	3.41
3	1977-late	6225.0 (24.8)	3000.6 (7.8)	2.07
3	1977-early	4287.0 (17.1)	6387.4 (16.7)	0.67
3	1976	8573.4 (34.1)	21020.7 (55.0)	0.41
3	1975	1312.7 (5.2)	6453.5 (16.9)	0.20

Figure 7. Relationship between P/B ratio and year-class for *Tagelus plebeius* at Lynnhaven Inlet, Virginia.

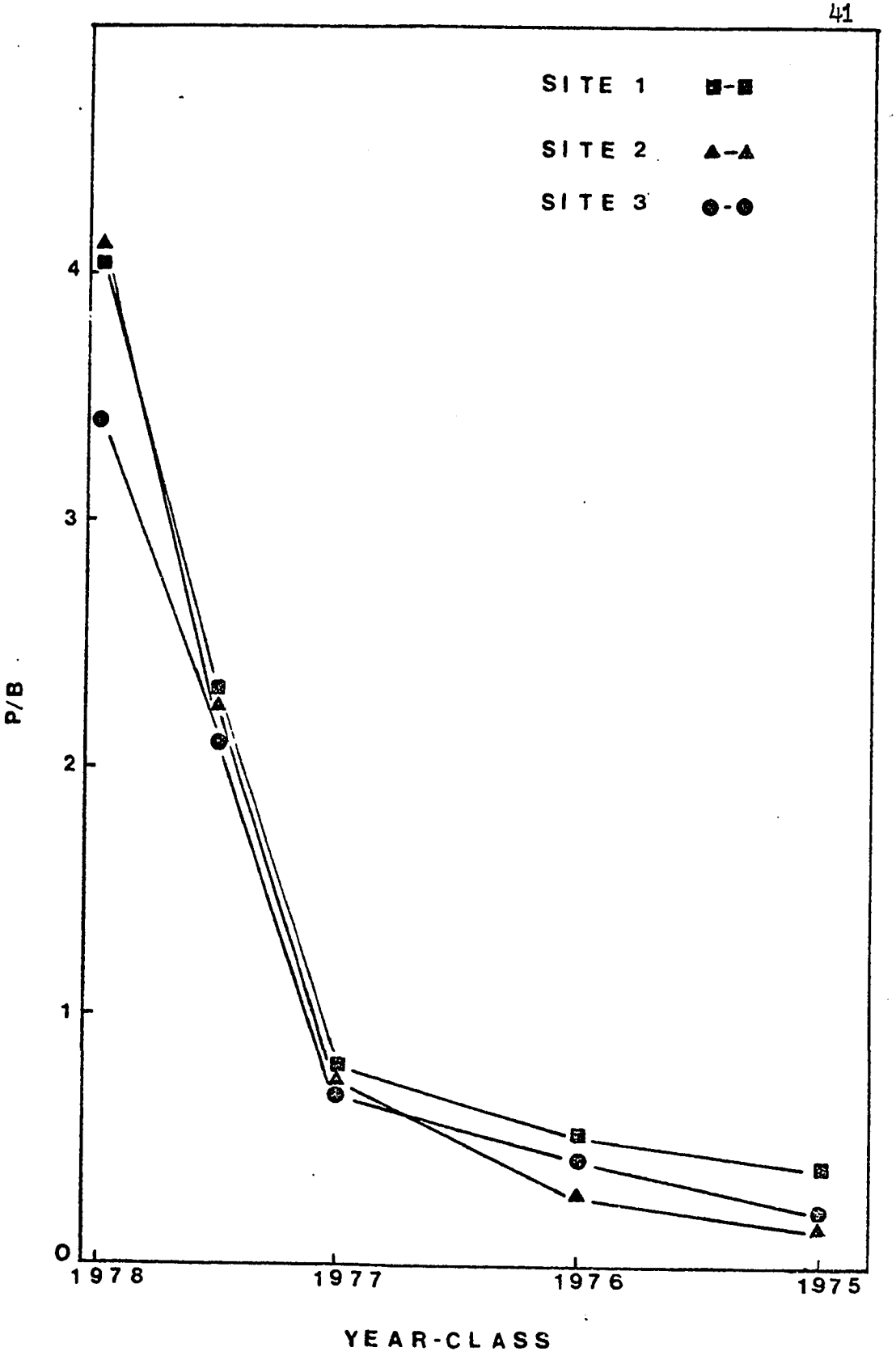


Table 15. Annual production (P), mean annual biomass (B), and P/B ratios for all sites computed at varying sample intervals. Percent change from the six week sample interval is given in parentheses for larger sample intervals.

Site	Sample interval (weeks)	P ($mg\ m^{-2}\ yr^{-1}$)	B ($mg\ m^{-2}$)	P/B
1	6	18324.3	27219.2	0.67
1	12	19117.5 (4)	28060.7 (3)	0.68 (1)
1	24	19842.3 (8)	28287.9 (4)	0.70 (4)
1	52	16038.0 (12)	26374.2 (3)	0.61 (9)
2	6	28688.4	53308.2	0.54
2	12	30078.5 (5)	54897.0 (3)	0.55 (2)
2	24	31443.3 (10)	57470.6 (8)	0.55 (2)
2	52	23262.0 (19)	55824.5 (5)	0.42 (22)
3	6	25111.8	38246.4	0.66
3	12	25148.8 (0)	38884.3 (2)	0.65 (2)
3	24	25703.2 (2)	39316.1 (3)	0.65 (2)
3	52	16624.9 (34)	37118.4 (3)	0.45 (32)

using six week intervals (assuming the six week interval displays the best estimate), the difference when using the 12 week interval is less than 5, 3, and 2% for P, B, and P/B, respectively. Even with 24 week intervals the differences are always less than 10, 8, and 2% for P, B, and P/B. However, the 52 week interval shows a maximum difference of 34, 5, and 32% for P, B, and P/B.

DISCUSSION

Biology and Environmental Variables

The only other major study of the biology of Tagelus plebeius was that of Holland and Dean (1977a and 1977b). They found that Tagelus plebeius made up 93.0% of the intertidal infaunal biomass but only 3.2% of the total number of individuals in North Inlet Estuary, near Georgetown, South Carolina. They examined populations at several different tidal levels and in widely different sediment types. The largest concentrations of Tagelus plebeius were located at 0 to 25 cm above mean low water (MLW), in sediments having a M_d of 2.10 to 2.40 ϕ, and composed of 2 to 15% silts and clays. The annual range of water temperature was 8 to 29°C, while salinity averaged about 28°/oo with lows of 20°/oo recorded during wet periods. They classified Tagelus plebeius as an infaunal suspension feeder.

Fraser (1967) investigated the biology of Tagelus divisus in a shallow subtidal environment in Biscayne Bay, Florida. The M_d of the sediment was between 1.4 and 2.3 ϕ with about 10% silts and clays. The range of temperature in the study area was from 19.5 to 30°C, while salinity ranged between 33.0 and 37.5°/oo. Tagelus divisus is also described as a suspension feeder.

Peterson (1977) described Tagelus californianus as a suspension feeder and one of the six most abundant macrofaunal species found in the Magu Lagoon sand community in Southern California. The

temperature range was from 13 to 22°C, while salinity remained fairly constant at 34°/oo. The sediment was described as coarse sand (1 to 40% larger than 0 ϕ by weight).

Maurer et al. (1974) classify both Tagelus plebeius and Tagelus divisus as true estuarine species, living in silt-clay through medium sand substrates with salinities in the range from 13 to 30°/oo and 15 to 25°/oo, respectively. They also classify both as deposit feeders, but this is incorrect (Pohlo, 1966; Fraser, 1967; Holland and Dean, 1977a).

Wass (1972) lists Tagelus plebeius as an abundant upper mesohaline and lower polyhaline species living in silty sand and in water depths from 0 to 5 feet.

The Tagelus plebeius population at Lynnhaven Inlet fits well within the ranges of environmental conditions found by other investigators, though temperatures were lower in the present study. The sediment is fine to medium sand with low silt-clay percentages. The temperature range is from 1.0°C in March to a high of 26.5°C in early September. The salinity range was 13.0 to 21.0°/oo.

Statistically significant differences were found between sites for RPD, Mz, M_d, and σ_I (Table 2). However, noting the very small real differences between these values at the sites, and recalling the wide variance in these variables reported by other investigators (Allen, 1954; Pfitzenmeyer, 1961; Holland and Dean, 1977a), these statistical differences probably have no biological significance for the Tagelus plebeius populations at the three sites in Lynnhaven Inlet. The same is true for the statistically

significant seasonal differences noted in the sediment variables at all three sites.

This conclusion is supported in part by the lack of a significant correlation between any of the three bivalve species and the sediment variables. This does not mean that bivalve species are not sensitive to their substrate composition (Gray, 1974). There is, however, not enough range within the sediment variables at the three sites to affect the abundance of the three species present. Still, the abundance of both Tagelus plebeius and Mya arenaria correlate significantly with salinity ($p < 0.05$) at site 3. The correlation is negative, meaning that the abundance of these bivalves was high when the salinity was low. An explanation for this lies in the fact that low salinities were measured in April, just as the juveniles of the year for both species were first sampled. Significant correlations between the abundance of the bivalves as a group and salinity are explained with the same logic. Though the seasonal change in the silt-clay percentage and σ_I is small, both variables reach their maximum values near April when bivalve abundance is near a maximum.

Salinity and temperature were the only measured environmental variables which displayed great seasonal change. The deep infaunal environment buffers the change in both salinity and temperature (Johnson, 1965; Jansson, 1967; Johnson, 1967; Holland and Polgar, 1976). Thus, as a deep burrowing infaunal bivalve, Tagelus plebeius would experience a reduced range of temperature and salinity over tidal and seasonal cycles.

Age Composition

The number of year-classes present did not vary between the sites but did vary seasonally. Discounting the bimodal recruitment in 1977, the population was composed of three year-classes in the fall and winter. Four year-classes were present from mid-spring to mid-summer when the spat of the year had settled and before the oldest year-class disappeared. This is in agreement with the low intertidal populations studied by Holland and Dean (1977b).

The bimodal recruitment in 1977 is difficult to explain. Holland and Dean (1977b) found only two out of phase juveniles, the spring recruitment being the normal situation in South Carolina. No other field data are available to support or deny a bimodal recruitment for this species.

No data are available on the annual cycle of gametogenesis for Tagelus plebeius, though Chanley and Castagna (1971) report apparently mature gametes present from June through November in specimens collected from Cedar Island on the Eastern Shore of Virginia and beaches near Gloucester Point, Virginia. Their attempts to spawn Tagelus plebeius in the laboratory were successful only in late August and September, when adults were subjected to fluctuating temperatures between 20 and 32°C. A natural field spawning at this time could support a late fall or winter recruitment, as reported in the present study. Also, a spawning in late November or December could support a spring recruitment.

Fraser (1967) found winter spawning from December to March in Tagelus divisus with the smallest juveniles found from late April

through June. The settlement corresponds with the spring settlement reported in the present study and by Holland and Dean (1977b).

Table 16 lists some bivalves with possible bimodal or unimodal spawning. Both Mya arenaria and Macoma balthica show bimodal spawning in the Chesapeake Bay area.

Investigators cite many factors which might regulate gametogenesis in marine invertebrates. These include temperature, photoperiod, salinity, abundance of food, and chemical factors (Giese and Pearse, 1974). In addition, though one of these factors may regulate gametogenesis, another may be of primary importance in providing the ultimate spawning stimulus (Purchon, 1977).

The factor of greatest importance to Tagelus plebeius is not clear, though changes in water temperature may be the primary regulator (Gunter, 1957; Kinne, 1970).

Holland and Dean (1977b) observed that high juvenile densities corresponded with areas of high adult density. In the present study young year-classes (1978, 1977-late) were more abundant at site 3 while old year-classes (1977-early, 1976) were more abundant at site 2. Not enough data are available to determine if this is the result of attraction of spat to areas with high adult density or if the spat may be attracted by some property of the substrate. Scheltema (1974) reviews the topic of biological interactions determining the larval settlement in marine invertebrates.

Size Composition and Growth

Larval development under laboratory conditions was described by

Table 16. Intertidal and shallow subtidal bivalves with known bimodal or unimodal spawnings.

Species	Bimodal spawning	Location	Environment[4]	Source
Tagelus plebeius	yes[2]	Lynnhaven Inlet, Virginia	I	Present Study
Tagelus plebeius	no[2]	Georgetown, South Carolina	I	Holland & Dean, 1977b
Dosinia elegans	yes[3]	Biscayne Bay, Florida	SS	Moore & Lopez, 1970
Mya arenaria	no[1]	Roskilde Fjord, Denmark	SS	Munch-Petersen, 1973
Mya arenaria	yes[3]	Cape Ann, Massachusetts	I	Brousseau, 1978
Mya arenaria	yes[1]	Solomons, Maryland	SS	Pfitzenmeyer, 1965
Mya arenaria	yes[2]	Tred Avon River, Maryland	SS	Shaw, 1965
Macoma balthica	no[2]	Ythan Estuary, Scotland	I	Chambers & Milne, 1975
Macoma balthica	no[2]	Lynher Estuary, England	I	Warwick & Price, 1975
Macoma balthica	no[1]	Falmouth, Maine	I	Gilbert, 1978
Macoma balthica	no[2]	Grevelingen Estuary, The Netherlands	I, SS	Wolff & de Wolf, 1977
Macoma balthica	yes[2]	Tred Avon River, Maryland	SS	Shaw, 1965
Macoma phenax	no[2]	Tred Avon River, Maryland	I	Shaw, 1965
Macoma nasuta	no[1]	Tomales Bay, California	I	Rae, 1978
Macoma secta	yes[1]	Tomales Bay, California	I	Rae, 1978

[1]Evidence from gonad examination

[2]Evidence from field settlement data

[3]Evidence from gonad examination and field settlement data

[4]I = intertidal, SS = shallow subtidal

Chanley and Castagna (1971). The larvae complete pelagic development at a smaller size than that reported for any known bivalve (155 to 170 u, in 8 to 11 days). Data on development immediately after settlement up to the 19 to 20 mm size are not available.

The juveniles in South Carolina (Holland and Dean, 1977b) were first collected in June at a S_L of about 19 mm, while in the present study juveniles were first collected in mid-April with S_Ls of about 20 mm. In both studies, most growth took place prior to the first winter with decreased growth in older year-classes. In South Carolina, Tagelus plebeius grew faster in low intertidal areas (0 to 25 cm above MLW) than in high intertidal areas (55 to 70 cm above MLW). The maximum S_Ls in the low areas were reported to be significantly greater than in high areas; 90 and 70 mm, respectively. In the present study, the sites were about 42 cm above MLW. There was no significant difference between the Ford-Walford growth lines for the three sites. The final S_Ls were about 88 mm. Fraser (1967) reported similar rapid growth for Tagelus divisus though the maximum adult size for the species was only about 32 mm.

Holland and Dean (1977a) found that larger specimens maintained deeper burrows. A 22 mm clam had a burrow of only 21 cm, while a 58 mm clam could have a burrow as deep as 70 cm. Therefore, rapid growth appears to be an important method of predator evasion.

The American oystercatcher, Halmatopus palliatus palliatus and sting rays such as Dasyatis sabena and Dasyatis americana were reported as predators by Holland and Dean (1977b). Their laboratory studies indicated that the simple dog whelk, Busycon

carica, could burrow to a depth of 15 cm in pursuit of Tagelus plebeius and that this predator was found burrowed to depths of 30 cm in the field. Under laboratory conditions the blue crab, Callinectes sapidus, and the stone crab, Menippe mercenaria were also able to extract Tagelus plebeius from shallow burrows.

In the present study, numerous shore birds were observed on the sand flat at low tide throughout the year, and Callinectes sapidus was often found in small tide pools or seen near the sample sites at high tide. No actual predation was observed in the field.

Clams of the genus Tagelus have gaping shells which can not be totally closed to protect the flesh. Thus, rapid growth and the associated deeper burrow allows greater separation from predators at the sediment water interface (Virnstein, 1977). In addition, the fluctuations in salinity and temperature are buffered, reducing the physical stress normally associated with intertidal environments (Newell, 1970).

Biomass and Production

The biomass of the Tagelus plebeius populations at Lynnhaven Inlet displayed no significant seasonal change, though the value at site 2 (53308 mg m^{-2}) was significantly greater than at sites 1 (27219 mg m^{-2}) and 3 (38246 mg m^{-2}). Though the annual P was different at each site, the difference was not significant. Total annual P at the sites was 18324, 28688, and 25112 mg $m^{-2}yr^{-1}$ for sites 1, 2, and 3, respectively. The P/B ratio at site 2 (0.54) was lower than at sites 1 (0.67) and 3 (0.66).

The annual P, B, and P/B values estimated for Tagelus plebeius may be compared with those given by other researchers studying intertidal or shallow subtidal bivalves (Table 18). The values range from -0.74 to 743.8 g $m^{-2}yr^{-1}$, 0.14 to 370.0 g m^{-2}, and -0.25 to 2.61 for P, B, and P/B, respectively. The estimates for Tagelus plebeius in the present study fall well within these ranges. Though the P and B values may be quite different, even for the same species, the P/B ratios fall within a narrow range.

Chambers and Milne (1975) suggest that for North-Temperate marine and estuarine bivalves with life spans of several years, annual P/B in most cases falls between 1.5 and 2.5. Waters (1977) proposes that the P/B ratio is a function of voltinism (the number of generations produced per year), and may be assumed within a range if voltinism is known. Annual P/B ratios for zoobenthos would average 1.7, 4.5, 5.4, and 8.3 for long-lived molluscs, univoltine species, bivoltine species, and multivoltine species, respectively.

Certainly Waters' estimate for long-lived molluscs falls within the range of 1.5 to 2.5 given by Chambers and Milne (1975). However, if some of these long-lived molluscs, such as Mya arenaria and Macoma balthica, are categorized as univoltine or bivoltine species according to Waters' classification, then the P/B ratios actually determined from field studies would be too low. The published P/B ratios (Table 17) support placement of these bivalves in the group with the lower P/B ratio. But to categorize these molluscs separately according to life span is not following the rules of voltinism originally proposed.

Table 17. Annual production (P), mean annual biomass (B), and P/B ratios for intertidal and shallow subtidal bivalves.

Species	P ($g\ m^{-2}\ yr^{-1}$)	B ($g\ m^{-2}$)	P/B	Source
Tagelus divisus[a]	43.02[b]	16.47[b]	2.61	Fraser, 1967
Tagelus plebeius	-	16.92[b]	-	Holland & Dean, 1977a
Tagelus plebeius	24.0	39.1	0.61	Present Study
Crassostrea virginica	743.0[c]	370.0[c]	2.01	Dame, 1976
Mercenaria mercenaria	4-14	8-50	0.17-0.50	Hibbert, 1977b
Macoma balthica	-0.7 to 3.4	0.14 to 2.9	-0.2 to 1.9	Wolff & de Wolf, 1977
Macoma balthica	0.31	0.34	0.91	Warwick & Price, 1975
Macoma balthica	9.06[b]	4.37[b]	2.07	Chambers & Milne, 1975
Macoma balthica	1.74[b]	1.12[b]	1.54	Burke & Mann, 1974
Mya arenaria	10.44[b]	4.10[b]	2.54	Burke & Mann, 1974
Mya arenaria	2.66	5.54	0.48	Warwick & Price, 1975
Cerastoderma edule	29-71	18-65	0.62 to 2.5	Hibbert, 1977b
Scrobicularia plana	0.48	2.15	0.22	Warwick & Price, 1975

[a]Shallow subtidal

[b]Converted from dry wt to AFDW assuming 1 g dry wt = 0.9 g AFDW (Waters, 1977)

[c]Converted from kcal to AFDW assuming 1 kcal = 0.18 g AFDW (Waters, 1977)

Few production studies have been conducted at the community level for macrobenthic invertebrates. However, of those available (Table 18), the trend is for decreasing production with increasing depth (Warwick et al., 1978). The values for B and P/B also show a similar trend though there are some exceptions. Sanders' (1956) values are probably too high for P as only small organisms of 0.2 g or less were used in his computations. Including the heavier specimens would have increased B with a corresponding decrease in P/B. The P/B ratios in Tagelus plebeius vary considerably with year-class. Young year-classes have ratios much higher than old year-classes.

Varying the sample interval had little effect on annual P, B, or P/B until the 52 week interval was used. Here the results become too extreme. In future studies of Tagelus plebeius, either 6, 12, or at the most 24 week intervals should be adequate to compute annual production. This assumes that the sample size is large enough to separate year-classes. If P is estimated from the P/B ratio after sampling to determine B, care should be taken to record the size of specimens in the samples. With size data available, an estimate of age can be made, allowing the researcher to use an appropriate P/B ratio from Figure 7. Note that P/B varies from greater than four to almost zero depending on the age structure of the population.

Researchers have suggested similar reasons for high values of benthic secondary production in shallow estuaries. In San Francisco Bay, California, Nichols (1977) states that the high production is maintained by: (1) tidal transport of salt marsh detritus, (2) the continuous tide and wave action resuspending surface sediment,

Table 18. Annual production (P), mean annual biomass (B), and P/B ratios for benthic invertebrate communities.

Community type	P ($g\ m^{-2}\ yr^{-1}$)	B ($g\ m^{-2}$)	P/B	Water depth	Source
Macoma	57.43	36.26	1.58	I[d]	Wolff & de Wolf, 1977
Macoma	13.31	13.24	1.01	I	Warwick & Price, 1975
Macoma/Gemma	85.55[a]	19.00	4.50[b]	I	Nichols, 1977
Venus	25.82	45.79	0.56	14 m	Warwick et al., 1978
Nephtys/Yoldia	26.64[c]	10.71[c]	2.44	18 m	Sanders, 1956
Pontoporeia	6.08[c]	3.88[c]	1.57	46 m	Cederwall, 1977
Brissopsis/Amphiura	1.74	3.98	0.44	80 m	Buchanan & Warwick, 1974

[a]Estimated assuming P/B = 4.5

[b]Assumed

[c]Converted from dry wt to AFDW assuming 1 g dry wt = 0.9 g AFDW (Waters, 1977)

[d]I = intertidal

detritus, and benthic diatoms, (3) diatoms present on the mud surface during a large part of the year, and (4) the plankton, treated sewage, and riverborne particulate matter in the water column. Thus, large amounts of potential food are often present and cycled through the system.

Wolff (1977) presents arguments similar to those of Nichols' (1977), however, he contrasts the benthic food budgets in the Grevelingen Estuary, The Netherlands, with those in American estuaries. In the Grevelingen Estuary the benthos depend mainly on the import of detrital material from the North Sea and in situ primary production. The benthic communities in American estuaries often receive the greatest portion of food from detritus material produced in adjacent salt marshes (Nixon and Oviatt, 1973).

Wolff and de Wolf (1977) found that in the Grevelingen Estuary, the period of immersion and current speed played an important role in governing production in suspension feeding bivalves. For Cardium edule and Mytilus edulis, production was higher where currents were stronger and immersion periods longer. No currents were measured in the present study, though the presence of small sand ripples on the sediment surface is probably indicative of bottom currents associated with wind, wave, and tidal action over the sand flat (Bird, 1969; Shepard, 1973).

The bivalves collected in the present study were all suspension feeders, able to take advantage of in situ primary production (phytoplankton or benthic diatoms suspended by water turbulence) or detrital material from adjacent salt marsh grasses. Low

concentrations of organic material in the sediment, probably due to current and wave activity, make it unlikely that reworking of the sediment by deposit feeders (Rhoads, 1973; McCall, 1977; Myers, 1977a and 1977b; Rhoads et al., 1977; Rhoads et al., 1978) would upset the burrows of Tagelus plebeius or Mya arenaria. As Tagelus plebeius and Mya arenaria are potential bimodal spawners, the possibility of maintaining the population through successful recruitment may be greater than if spawning took place on only one occasion.

By utilizing the protection of deep burrows in the intertidal zone, both Tagelus plebeius and Mya arenaria can evade many predators (e.g. crabs and fish) hunting at the sediment-water interface, while these same predators are subject to predation by birds if they remain visible on the sand flat at low tide.

The high annual P and B values computed for Tagelus plebeius in the present study are by no means assured in future studies. Numerous researchers indicate that intertidal and shallow subtidal invertebrates may have variable spawning and settlement success from year to year, often depending on one major settlement success to maintain the population over a long period (McIntyre, 1970; Beukema, 1974; Nichols, 1977; Simon and Dauer, 1977; Beukema et al., 1978)

CONCLUSIONS

The Lynnhaven Inlet, Virginia, Tagelus plebeius populations are living under environmental conditions similar to those reported by other researchers.

The abundance of Tagelus plebeius varied significantly between sites but did not vary significantly on a seasonal basis. Though statistically significant differences were found in the sediment variables either between sites or at the sites over the sample year, the differences were very small and were not considered to be biologically significant. In addition, no significant correlations were found between Tagelus plebeius abundance and any of the measured sediment variables.

The bimodal recruitment observed in 1977 was not repeated in 1978. Bimodal recruitment in this species has not previously been reported, though it has been observed in other bivalves in the Chesapeake Bay area (e.g. Mya arenaria, Macoma balthica).

The year-class composition was similar at all three sites. Excluding the bimodal settlement in 1977, there were three year-classes present in the fall and winter. Four year-classes were present from mid-spring to mid-summer when the spat of the year had settled and before the older year-class disappeared. Juveniles were more abundant at one site, while adults were more abundant at another.

Juveniles with S_Ls of 20 mm were collected in mid-April. They grew rapidly to a length of 53 mm in December. Greater than 50% of

the total shell growth was completed prior to the first winter.

Growth and maximum S_L did not vary significantly between sites. A maximum S_L of 88 mm was predicted from the Ford-Walford growth plot. This prediction agrees well with field observations. The increased burrow depth accompanying the rapid growth is important for survival in this species. Deep burrows provide protection from predators and serve to buffer changes in the temperature and salinity.

The total biomass of Tagelus plebeius was significantly different between sites but did not show a significant seasonal change. The annual P did show a significant seasonal change (high from January to June and lower at other times) but was not significantly different between sites. The P/B ratios were similar at the sites, though the value at site 2 was less than at sites 1 and 3. The P/B ratios were high in the young year-classes but declined to much lower values in the older year-classes.

The values of annual P, B, and P/B were well within the ranges reported in other studies for intertidal and shallow subtidal bivalves. However, the use of 12, 24, and 52 week sample intervals resulted in differences in the estimated values of P, B, and P/B. The differences were small for the 12 and 24 week intervals but very large when the 52 week interval was used. In future studies, the 6, 12, or 24 week intervals are considered acceptable, though the interval selected will depend on the goals of the investigation.

The high values of annual P and B are probably due to the large potential food supply at the Lynnhaven Inlet sites plus the absence of large deposit feeding invertebrates which might rework the sediment to

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such a degree that the burrows of Tagelus plebeius would be upset. Currents, wind, and wave action are probably important in keeping the organic material from building up on the sand flat and providing potential food for deposit feeders.

The values of annual P and B for Tagelus plebeius may fluctuate from year to year due to variable spawning or settlement success. Thus, the values found in the present study are not to be considered as constants.

Future ecological studies concerning this species should be conducted both in the laboratory and in the field. To define the complete energy budget for Tagelus plebeius, work should center on determining rates of respiration, assimilation, consumption, and excretion. Microscopic examination of the gonads on a seasonal basis would allow a more conclusive statement concerning the regularity of bimodal spawning as reported in this study. Estimates of the percentage of annual production in terms of flesh production and gamete production would also result from such an examination.

Field experiments would be useful in estimating the portion of the annual production that actually becomes available to predators (crabs, birds, and fish). Though Tagelus plebeius has no direct economic value, its great abundance and biomass are probably important to predators which may contribute directly to the Chesapeake Bay seafood industry.

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Appendix A

Means, standard deviations, and standard errors for all bivalve abundances, temperature, salinity, and sediment variables. Values are listed by sample date and site.

Total Bivalve Abundance
(*Tagelus plebeius*, *Mya arenaria*, *Mercenaria mercenaria*)

Date (1977-1978)	Site	Mean (No. m^{-2})	SD	SE
Dec. 3-5	1	64.7	47.6	21.3
	2	80.7	24.0	10.7
	3	52.7	6.4	2.9
Jan. 18-20	1	62.0	29.2	13.1
	2	69.3	32.2	14.4
	3	48.0	23.3	10.4
Mar. 4-6	1	53.3	28.9	12.9
	2	62.7	24.4	10.9
	3	42.0	18.9	8.5
Apr. 18-20	1	54.0	23.6	10.6
	2	80.0	28.0	12.5
	3	56.0	5.5	2.5
June 3-5	1	49.3	32.6	14.6
	2	67.3	29.8	13.3
	3	50.0	19.3	8.6
July 18-21	1	38.7	11.2	5.0
	2	54.7	15.6	7.0
	3	45.3	22.3	10.0
Sept. 2-4	1	38.7	18.0	8.0
	2	48.0	16.8	7.5
	3	37.3	18.8	8.4
Oct. 18-20	1	32.7	10.9	4.9
	2	43.3	17.2	7.7
	3	28.7	12.2	5.5
Dec. 3-5	1	32.0	9.6	4.3
	2	37.3	19.9	8.9
	3	24.0	11.4	5.1

Tagelus plebeius abundance

Date (1977-1978)	Site	Mean (No. m^{-2})	SD	SE
Dec. 3-5	1	30.0	16.3	7.3
	2	61.3	15.0	6.7
	3	49.3	6.0	2.7
Jan. 18-20	1	28.0	37.5	16.8
	2	56.0	26.6	11.9
	3	46.0	21.9	9.8
Mar. 4-6	1	25.3	17.1	7.6
	2	51.3	28.5	12.7
	3	39.3	18.8	8.4
Apr. 18-21	1	26.0	17.9	8.0
	2	56.0	23.5	10.5
	3	48.7	5.1	2.3
June 3-5	1	24.0	33.3	14.9
	2	51.3	32.8	14.7
	3	43.3	20.5	9.2
July 18-21	1	21.3	18.2	8.1
	2	46.0	14.4	6.4
	3	40.0	22.2	9.9
Sept. 2-4	1	18.7	9.3	4.2
	2	40.0	17.6	7.9
	3	34.0	18.9	8.5
Oct. 18-20	1	15.3	6.1	2.7
	2	37.3	19.1	8.5
	3	28.0	13.0	5.8
Dec. 3-5	1	14.7	11.7	5.2
	2	32.0	18.3	8.2
	3	22.7	11.9	5.3

Mya arenaria abundance

Date (1977-1978)	Site	Mean (No. m^{-2})	SD	SE
Dec. 3-5	1	33.3	35.2	15.7
	2	19.3	21.8	9.7
	3	0.0	0.0	0.0
Jan. 18-20	1	34.0	35.6	15.9
	2	12.7	13.0	5.8
	3	0.7	1.5	0.7
Mar. 4-6	1	26.7	21.2	9.5
	2	11.3	6.1	2.7
	3	0.0	0.0	0.0
Apr. 18-21	1	28.0	12.8	5.7
	2	23.3	13.1	5.9
	3	6.7	4.7	2.1
June 3-5	1	25.3	15.0	6.7
	2	15.3	6.5	2.9
	3	5.3	4.5	2.0
July 18-21	1	17.3	14.2	6.4
	2	8.0	3.0	1.3
	3	4.7	3.8	1.7
Sept. 2-4	1	19.3	13.2	5.9
	2	7.3	6.4	2.9
	3	1.3	1.8	0.8
Oct. 18-20	1	16.0	7.6	3.4
	2	4.7	3.8	1.7
	3	0.0	0.0	0.0
Dec. 3-5	1	16.7	7.7	3.4
	2	5.3	3.0	1.3
	3	0.7	1.5	0.7

Mercenaria mercenaria abundance

Date (1977-1978)	Site	Mean (No. m^{-2})	SD	SE
Dec. 3-5	1	1.3	3.0	1.3
	2	0.0	0.0	0.0
	3	3.3	3.3	1.5
Jan. 18-20	1	0.0	0.0	0.0
	2	0.7	1.5	0.7
	3	1.3	1.8	0.8
Mar. 4-6	1	1.3	1.8	0.8
	2	0.0	0.0	0.0
	3	2.7	1.5	0.7
Apr. 18-21	1	0.0	0.0	0.0
	2	0.7	1.5	0.7
	3	0.7	1.5	0.7
June 3-5	1	0.0	0.0	0.0
	2	0.7	1.5	0.7
	3	1.3	1.8	0.8
July 18-21	1	0.0	0.0	0.0
	2	0.7	1.5	0.7
	3	0.7	1.5	0.7
Sept. 2-4	1	0.7	1.5	0.7
	2	0.7	1.5	0.7
	3	2.0	3.0	1.3
Oct. 18-20	1	1.3	1.8	0.8
	2	1.3	3.0	1.3
	3	0.7	1.5	0.7
Dec. 3-5	1	0.7	1.5	0.7
	2	0.0	0.0	0.0
	3	0.7	1.5	0.7

RPD

Date (1977-1978)	Site	Mean (cm)	SD	SE
Dec. 3-5	1	3.0	0.9	0.4
	2	1.1	0.6	0.3
	3	0.6	0.2	0.1
Jan. 18-20	1	2.9	1.1	0.5
	2	0.6	0.3	0.1
	3	0.5	0.4	0.2
Mar. 4-6	1	2.2	1.1	0.5
	2	0.5	0.3	0.1
	3	0.5	0.4	0.2
Apr. 18-21	1	2.0	0.9	0.4
	2	0.5	0.4	0.2
	3	0.5	0.3	0.1
June 3-5	1	0.5	0.4	0.2
	2	0.4	0.4	0.2
	3	0.3	0.1	0.0
July 18-21	1	0.8	0.4	0.2
	2	0.3	0.2	0.1
	3	0.3	0.1	0.0
Sept. 2-4	1	0.8	0.3	0.1
	2	0.3	0.1	0.0
	3	0.3	0.1	0.0
Oct. 18-20	1	1.4	0.5	0.2
	2	0.7	0.1	0.0
	3	0.5	0.3	0.1
Dec. 3-5	1	2.9	0.9	0.4
	2	1.1	0.6	0.3
	3	0.6	0.2	0.1

Silt-clay Percentage

Date (1977-1978)	Site	Mean (% by wt)	SD	SE
Dec. 3-5	1	2.10	0.27	0.12
	2	2.15	0.66	0.30
	3	1.88	0.50	0.22
Jan. 18-20	1	2.80	1.34	0.60
	2	2.84	0.32	0.14
	3	2.73	0.92	0.41
Mar. 4-6	1	2.96	0.70	0.31
	2	4.16	0.75	0.34
	3	3.75	0.81	0.36
Apr. 18-21	1	4.11	0.76	0.34
	2	3.95	0.86	0.38
	3	4.04	0.97	0.43
June 3-5	1	3.50	1.11	0.50
	2	2.62	0.56	0.25
	3	2.09	0.61	0.27
July 18-21	1	2.20	0.64	0.29
	2	2.72	0.94	0.42
	3	2.12	0.28	0.13
Sept. 2-4	1	2.43	1.00	0.45
	2	2.47	0.34	0.15
	3	3.57	0.85	0.38
Oct. 18-20	1	2.24	1.13	0.51
	2	2.26	0.39	0.17
	3	3.21	1.54	0.69
Dec. 3-5	1	2.15	0.32	0.14
	2	2.19	0.65	0.29
	3	1.91	0.51	0.23

Organic Content Percentage

Date (1977-1978)	Site	Mean (% by wt)	SD	SE
Dec. 3-5	1	0.56	0.17	0.08
	2	0.49	0.08	0.04
	3	0.65	0.14	0.06
Jan. 18-20	1	0.38	0.17	0.08
	2	0.33	0.11	0.05
	3	0.20	0.06	0.03
Mar. 4-6	1	0.53	0.15	0.08
	2	0.92	0.37	0.17
	3	0.72	0.13	0.06
Apr. 18-20	1	0.60	0.13	0.06
	2	0.81	0.42	0.19
	3	0.56	0.21	0.09
June 3-5	1	0.78	0.26	0.12
	2	0.56	0.06	0.03
	3	0.55	0.14	0.06
July 18-21	1	0.37	0.04	0.02
	2	0.38	0.07	0.03
	3	0.31	0.05	0.02
Sept. 2-4	1	0.49	0.07	0.03
	2	0.46	0.03	0.01
	3	0.64	0.14	0.06
Oct. 18-20	1	0.51	0.07	0.03
	2	0.49	0.05	0.02
	3	0.48	0.14	0.06
Dec. 3-5	1	0.56	0.16	0.07
	2	0.49	0.08	0.07
	3	0.66	0.13	0.06

Mz

Date (1977-1978)	Site	Mean (ø)	SD	SE
Dec. 3-5	1	1.98	0.08	0.04
	2	2.00	0.17	0.08
	3	1.83	0.09	0.04
Jan. 18-20	1	2.04	0.04	0.02
	2	2.13	0.13	0.06
	3	1.91	0.27	0.12
Mar. 4-6	1	2.17	0.07	0.03
	2	2.13	0.13	0.06
	3	2.04	0.24	0.12
Apr. 18-20	1	2.17	0.18	0.08
	2	2.10	0.12	0.05
	3	2.04	0.23	0.10
June 3-5	1	2.36	0.19	0.08
	2	2.11	0.14	0.06
	3	1.90	0.22	0.10
July 18-21	1	2.33	0.10	0.04
	2	2.13	0.18	0.08
	3	1.92	0.25	0.11
Sept. 2-4	1	2.27	0.12	0.05
	2	2.15	0.13	0.06
	3	1.98	0.14	0.06
Oct. 18-20	1	2.34	0.13	0.06
	2	2.13	0.13	0.06
	3	1.96	0.20	0.09
Dec. 3-5	1	2.05	0.07	0.03
	2	2.01	0.17	0.08
	3	1.83	0.10	0.04

M_d

Date (1977-1978)	Site	Mean (ø)	SD	SE
Dec. 3-5	1	2.18	0.04	0.02
	2	2.13	0.25	0.11
	3	1.87	0.13	0.06
Jan. 18-20	1	2.23	0.03	0.01
	2	2.27	0.14	0.06
	3	1.96	0.30	0.13
Mar. 4-6	1	2.30	0.04	0.02
	2	2.25	0.16	0.07
	3	2.08	0.28	0.13
Apr. 18-20	1	2.32	0.12	0.05
	2	2.23	0.12	0.05
	3	2.09	0.28	0.13
June 3-5	1	2.40	0.14	0.06
	2	2.26	0.17	0.08
	3	1.96	0.25	0.11
July 18-21	1	2.38	0.09	0.04
	2	2.34	0.30	0.13
	3	1.97	0.34	0.15
Sept. 2-4	1	2.32	0.10	0.04
	2	2.31	0.14	0.06
	3	2.03	0.19	0.08
Oct. 18-20	1	2.43	0.15	0.07
	2	2.35	0.21	0.09
	3	1.99	0.26	0.12
Dec. 3-5	1	2.21	0.04	0.02
	2	2.13	0.24	0.11
	3	1.86	0.13	0.06

σ_I

Date (1977-1978)	Site	Mean (ø)	SD	SE
Dec. 3-5	1	0.92	0.07	0.03
	2	0.89	0.03	0.01
	3	0.87	0.02	0.01
Jan. 18-20	1	0.92	0.04	0.02
	2	0.86	0.06	0.03
	3	0.88	0.08	0.04
Mar. 4-6	1	0.83	0.09	0.04
	2	0.89	0.08	0.04
	3	0.86	0.13	0.06
Apr. 18-20	1	0.90	0.08	0.04
	2	0.90	0.09	0.04
	3	0.87	0.08	0.04
June 3-5	1	0.69	0.15	0.07
	2	0.88	0.08	0.04
	3	0.88	0.04	0.02
July 18-21	1	0.65	0.08	0.04
	2	0.90	0.10	0.04
	3	0.87	0.07	0.03
Sept. 2-4	1	0.69	0.07	0.03
	2	0.84	0.07	0.03
	3	0.89	0.03	0.01
Oct. 18-20	1	0.67	0.09	0.04
	2	0.89	0.06	0.03
	3	0.90	0.11	0.05
Dec. 3-5	1	0.89	0.06	0.03
	2	0.89	0.04	0.02
	3	0.88	0.02	0.01

Temperature and Salinity

The mean, standard deviation, and standard error for the three sites (combined) for each sample date.

Date (1977-1978)	Temperature (°C)			Salinity (°/oo)		
	Mean	SD	SE	Mean	SD	SE
Dec. 3-5	11.7	0.3	0.2	19.3	0.6	0.3
Jan. 18-20	4.8	0.3	0.2	13.8	0.3	0.2
Mar. 4-6	1.3	0.3	0.2	15.3	0.3	0.2
Apr. 18-20	10.2	1.0	0.6	13.5	0.5	0.3
June 3-5	19.5	1.0	0.6	14.3	0.3	0.2
July 18-21	24.7	0.8	0.5	17.5	1.3	0.8
Sept. 2-4	25.7	0.8	0.5	19.5	1.3	0.8
Oct. 18-20	16.5	0.5	0.3	21.5	0.5	0.3
Dec. 3-5	12.5	0.5	0.3	19.5	0.5	0.3

Appendix B

Analysis of covariance tables. Values computed according to Dixon (1975).

Testing for differences in Ford-Walford growth lines

Source of Variance	Degrees of Freedom	Sum of Squares	Mean Squares	F-Value
Equality of Adj. cell means	2	0.18	0.09	0.00^{ns}
Zero Slope	1	193.36	293.36	10.63^{*}
Error	5	137.95	27.59	
Equality of Slopes	2	6.38	3.19	0.07^{ns}
Error	3	131.58	43.86	

$^{*}p < 0.05$

^{ns}Not significant

Testing for differences in S_L to AFDW regression lines. Each site is tested for significant differences in the lines over the sample year.

Source of Variance	Degrees of Freedom	Sum of Squares	Mean Squares	F-Value
Site 1				
Equality of Adj. cell means	8	0.24	0.03	7.53***
Zero Slope	1	47.76	47.76	11912.30***
Error	262	1.05	0.00	
Equality of Slopes	8	0.26	0.03	10.64***
Error	254	0.79	0.00	
Site 2				
Equality of Adj. cell means	8	0.84	0.10	12.54***
Zero Slope	1	123.31	123.31	14799.82***
Error	558	4.65	0.01	
Equality of Slopes	8	1.05	0.13	20.11***
Error	550	3.60	0.01	
Site 3				
Equality of Adj. cell means	8	0.70	0.09	16.42***
Zero Slope	1	115.61	115.61	21628.69***
Equality of Slopes	8	0.80	0.10	27.98***
Error	432	1.55	0.00	

*** $p < 0.001$

Testing for differences in S_L to AFDW regression lines. Each site is tested against the other sites on each sampling date to determine significant differences between sites.

Source of Variance	Degrees of Freedom	Sum of Squares	Mean Squares	F-Value
Dec. 3-5(1977)				
Equality of Adj. cell means	2	0.01	0.01	0.85^{ns}
Zero Slope	1	58.13	58.13	6847.54^{***}
Error	188	1.60	0.01	
Equality of Slopes	2	0.01	0.01	0.83^{ns}
Error	186	1.58	0.01	
Jan. 18-20				
Equality of Adj. cell means	2	0.02	0.01	1.36^{ns}
Zero Slope	1	38.31	38.31	5443.72^{***}
Error	159	1.12	0.01	
Equality of Slopes	2	0.06	0.03	4.13^{*}
Error	157	1.06	0.01	
Mar. 4-6				
Equality of Adj. cell means	2	0.00	0.00	3.35^{*}
Zero Slope	1	22.78	22.78	33703.32^{***}
Error	150	0.10	0.00	
Equality of Slopes	2	0.00	0.00	2.13^{ns}
Error	148	0.10	0.00	

Source of Variance	Degrees of Freedom	Sum of Squares	Mean Squares	F-Value
Apr. 18-21				
Equality of Adj. cell means	2	0.01	0.00	0.23^{ns}
Zero Slope	1	87.44	87.44	7431.12^{***}
Error	157	1.85	0.01	
Equality of Slopes	2	0.00	0.00	0.12^{ns}
Error	155	1.84	0.01	
June 3-5				
Equality of Adj. cell means	2	0.00	0.00	0.32^{ns}
Zero Slope	1	34.52	34.52	12875.20^{***}
Error	144	0.39	0.00	
Equality of Slopes	2	0.01	0.00	1.60^{ns}
Error	142	0.38	0.00	
July 18-21				
Equality of Adj. cell means	2	0.02	0.01	5.96^{**}
Zero Slope	1	24.41	24.41	17861.31^{***}
Error	132	0.18	0.00	
Equality of Slopes	2	0.00	0.00	1.15^{ns}
Error	130	0.17	0.00	
Sept. 2-4				
Equality of Adj. cell means	2	0.07	0.04	10.56^{***}
Zero Slope	1	13.33	13.33	3862.61^{***}
Error	121	0.42	0.00	
Equality of Slopes	2	0.07	0.04	12.67^{***}
Error	119	0.35	0.00	

Source of Variance	Degrees of Freedom	Sum of Squares	Mean Squares	F-Value
Oct. 18-20				
Equality of Adj. cell means	2	0.01	0.00	2.28^{ns}
Zero Slope	1	6.49	6.49	4782.77^{***}
Error	106	0.14	0.00	
Equality of Slopes	2	0.02	0.01	9.07^{***}
Error	104	0.12	0.00	
Dec. 3-5(1978)				
Equality of Adj. cell means	2	0.04	0.02	6.01^{**}
Zero Slope	1	3.20	3.20	964.21^{***}
Error	97	0.32	0.00	
Equality of Slopes	2	0.00	0.00	0.25^{ns}
Error	95	0.32	0.00	

^{ns}Not significant

$^{*}p < 0.05$

$^{**}p < 0.01$

$^{***}p < 0.001$

Appendix C

Kruskal-Wallis analysis of variance tests with associated multiple comparison tests. The Kruskal-Wallis test is computed according to Nie *et al.* (1975), while the multiple comparison tests are computed according to Wilcoxon and Wilcox (1964) and Langley (1970).

Kruskal-Wallis H statistic and multiple comparison test for all variables. Testing for significant differences between sites. The line below the sites in the multiple comparison test indicates no significant difference between the sites underlined.

Variable	H	Multiple comparison test	
All Bivalves	11.7**	2 1 3 *	2 1 3 **
Tagelus plebeius	34.2**	2 3 1 *	2 3 1 **
Mya arenaria	64.0**	1 2 3 *	1 2 3 **
Mercenaria mercenaria	4.9	ns	ns
RPD (cm)	49.7**	1 2 3 *	1 2 3 **
Silts-clays (%)	0.7	ns	ns
Organic content (%)	0.1	ns	ns
Mz (ø)	33.0**	1 2 3 *	1 2 3 **
M_d (ø)	39.0**	1 2 3 *	1 2 3 **
O_I	10.1**	2 3 1 *	2 3 1 **
Temperature (°C)	0.3	ns	ns
Salinity (°/oo)	0.2	ns	ns

ns Not significantly different

* $p < 0.05$

** $p < 0.01$

Kruskal-Wallis H statistic and multiple comparison test for differences in the abundance of each year-class between sites over the sample year.

Year-class	H	Multiple comparison test	
1978	12.2^{**}	3 2 1 *	3 2 1 **
1977-late	11.7^{**}	3 2 1 *	3 2 1 **
1977-early	18.3^{**}	2 3 1 *	2 3 1 **
1976	13.6^{**}	2 3 1 *	2 3 1 **
1975	3.0	ns	ns

^{ns}Not significantly different

$^{*}p < 0.05$

$^{**}p < 0.01$

Kruskal-Wallis H statistic and multiple comparison test for differences in the S_Ls of each year-class between sites over the sample year.[a]

Year-class	H	Multiple comparison test
1978	0.082	ns
1977-late	0.004	ns
1977-early	0.006	ns
1976	0.059	ns
1975	0.284	ns

[a]No significant differences were noted in any of these tests.

ns Not significantly different

Kruskal-Wallis H statistic and multiple comparison test for differences in the biomass of Tagelus plebeius between sites and over the sample year.

Between sites	H	Multiple Comparison test	
Biomass between sample dates	19.9**	2 3 1 *	2 3 1 **
Between seasons			
Biomass between sample dates	5.13	ns	ns

ns Not significantly different

* $p < 0.05$

** $p < 0.01$

Kruskal-Wallis H statistic and multiple comparison test for differences in the total production between sample dates. The test is given for significant differences between sites and for significant differences over the sample year.

Between sites	H	Multiple comparison test
Total P between sample dates	0.195	ns
Between seasons		
Total P between sample dates	20.36**	

Apr-June Jan-Mar Oct-Dec Sept-Oct Mar-Apr July-Sept June-July Dec-Jan
(78) (77)

ns Not significantly different

* $p < 0.05$

** $p < 0.01$

AUTOBIOGRAPHICAL STATEMENT

Mark James Grussendorf was born in Great Lakes, Illinois on October 9, 1948, the second son of a career Marine Corps Officer. His father's career necessitated numerous family relocations spanning coast to coast. Mark graduated from South Salem High School, Salem, Oregon in June 1966. Having accepted an appointment to the U.S. Naval Academy, midshipman training commenced during the summer of 1966. Midshipman Grussendorf declared a second major in Oceanography in addition to the mandatory Naval Science, and as a diversion participated in the school's cross-country program.

Mark Grussendorf was commissioned as an Ensign in the U.S. Navy on graduation day in June 1970. The summer of 1970 found Ensign Grussendorf in Pensacola, Florida for Naval Flight Training. At the end of nine months, Bombardier-Navigator "Wings" were awarded and Ensign Grussendorf was assigned to N.A.S. Oceana, Virginia for Flight Squadron Training in the Navy's A-6 jet bomber. After training Ensign Grussendorf received his first shipboard assignment on the carrier U.S.S. John F. Kennedy. Ltjg. Grussendorf completed two Mediterranean Sea cruises aboard the carrier and then accepted a position as Flight Instructor in Pensacola, Florida.

In June 1975, Lt. Grussendorf departed the Navy in order to undertake graduate studies at Old Dominion University, Institute of Oceanography, Norfolk, Virginia. Between September 1975 and December 1978, Mark Grussendorf for academic excellence was bestowed an Old Dominion University Fellowship, a membership in the Honor Society of Phi Kappa Phi, and a listing in Who's Who Among Students in American Universities and Colleges.